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

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ABSTRACT

The majority of American Oystercatchers (*Haematopus palliatus*) in South

Carolina make their nests on narrow, elevated mounds of oyster shells deposited naturally

along the edges of bays by storms or formed artificially by boat wakes along the Atlantic

Intracoastal Waterway (AICW). I compared reproductive success of American

Oystercatchers nesting along the AICW with those nesting on naturally formed shell

mounds in Bulls Bay within the Cape Romain Region of South Carolina during the

breeding seasons of 2006 and 2007. I identified timing and causes of nest failure and

attributes of re-nesting. Hatching success (15%) and productivity estimates (0.25 chicks

per pair) were low and variable between locations and between years. Oystercatchers

nesting in Bulls Bay were the most successful and more nests hatched in 2006 compared

to 2007. Overwash was the primary cause of nest loss (59%) followed by predation

(14%). Birds re-nested frequently after nest failure.

In addition to studying reproductive success, I also examined attributes of

foraging oystercatchers during the breeding season. I compared percentage of time parent

oystercatchers were absent from the nest territory during low-tide foraging periods for

birds nesting along the AICW with those nesting in Bulls Bay. Parents in Bulls Bay

attended the nest site more frequently and fledged more chicks than parent oystercatchers

nesting along the AICW. I also examined attributes of oystercatchers foraging including

prey choice, searching times and handling times of prey in two primary oyster reefs

within the Region. More oystercatchers were observed foraging in Bulls Bay than in

Sewee Bay and eastern oysters (*Crassostrea virginica)* were the primary diet item

consumed during the breeding season.

ACKNOWLEDGMENTS

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CHAPTER ONE

INTRODUCTION

Long-lived shorebird species often demonstrate high adult survival and high variability in breeding success from year to year (Evans 1991). Variability in reproductive success may be caused by local factors such as inclement weather, predation, or poor food resources (Newton 1998). These factors can vary in their intensity between locations and among years and may be exacerbated by coastal development and human encroachment. For example, predation of shorebird nests by predators associated with humans has been identified as a source of nest failure in coastal ecosystems (Sabine et al. 2006; McGowan et al. 2005). Disturbance to nesting birds by humans has also negatively influenced reproductive success (Jeffery 2005). As human populations increase in coastal areas, threats to coastal nesting species including habitat loss and disturbance during the breeding season may contribute to reduced productivity in beach nesting birds. The human population along the United States coasts is currently increasing and is estimated to increase to 165 million in the year 2015 (Culliton 1998). Population densities are highest on the East Coast and the population of coastal South Carolina is growing at a rate of ca. 1% to 3% per year (Allen & Lu 2003). With rapid human population growth in these coastal settings, an understanding of shorebird populations and reproductive parameters are needed in order to design strategies for their conservation.

A shorebird that may be vulnerable to coastal development along the southeastern coast is the American Oystercatcher (*Haematopus palliatus*). This coastal nesting species experiences highly variable reproductive success among years and among locations and

is intolerant to high levels of disturbance (Sabine et al. 2006). Although oystercatchers are long-lived and demonstrate variable breeding success, the lifetime reproductive success for this species is unknown (Nol & Humphrey 1994). Understanding population trends, especially aspects related to reproductive success is necessary for management and conservation of this species.

The American Oystercatcher breeds along the Atlantic Coast from Massachusetts to Florida (Humphrey 1990). They nest on barrier beach islands, salt marshes, dredge spoils and shell mounds (Lauro and Burger 1989; Toland 1992; Wilke et al. 2007). Oystercatchers scrape shallow depressions in the substrate and normally lay 2-3 eggs. Both adults incubate the clutch for approximately 27 days. South Carolina supports over 400 pairs of breeding oystercatchers, the majority of which nest on washed oyster shell mounds within the Cape Romain Region of the state (Sanders et al. 2008). Oystercatchers have laterally compressed bills and feed almost exclusively on shellfish and marine invertebrates found in exposed mudflats, intertidal areas, and shellfish reefs (Nol and Humphrey 1994). Because of this specialized diet that prohibits chicks from obtaining food on their own, parents will provision the young up to 60 days after hatching (Nol and Humphrey 1994). They first breed at 3 to 5 years of age, are monogamous and demonstrate nesting site fidelity.

I examined the reproductive success of American Oystercatchers nesting on the central coast of South Carolina. Specifically, I examined factors associated with the timing and causes of nest failure as well as attributes of foraging behavior during the breeding season. Measurements of annual fecundity in this species and identification of causes of nest failures are needed to (1) understand which factors may be contributing to

low reproductive rates and (2) design management strategies and set conservation goals. Understanding the relationship of fecundity and foraging ecology also will assist managers with where to target habitat protection and, if needed, enhancement.

Chapter two of this thesis, "Reproductive Success of American Oystercatchers in the Cape Romain Region, South Carolina", examines the reproductive ecology of American Oystercatchers nesting in two different habitat types within the Cape Romain Region. The first habitat type included nests that occurred on naturally formed shell mounds in Bulls Bay within the Cape Romain National Wildlife Refuge while the second habitat type included nests that occurred on shell mounds that formed primarily from boat wakes along the Atlantic Intracoastal Waterway. I measured hatching success and fledging success, and identified causes and timing of nest failure and chick loss during the 2006 and 2007 breeding seasons.

Chapter three of this thesis, "Foraging Behavior of American Oystercatchers During the Breeding Season in the Cape Romain Region, South Carolina", examines the foraging behavior and diet of oystercatchers during the breeding season. I compared the percentage of time parent oystercatchers were absent from their nesting territory in two different locations during the foraging period and related that time to reproductive success in 2006. I also compared prey selection and foraging efficiency including searching times and handling times of oystercatchers feeding in two different primary oyster reefs within the Cape Romain Region in 2007.

Identifying and understanding the connection between foraging ecology and reproductive success of this species is important for conserving habitat that this species requires for both nesting and feeding. It is imperative to investigate causes of nest failure

and poor productivity of these shorebirds, and to identify areas of positive growth of the American Oystercatcher population in South Carolina.

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CHAPTER TWO

REPRODUCTIVE SUCCESS OF AMERICAN OYSTERCATCHERS IN THE CAPE
ROMAIN REGION, SOUTH CAROLINA

Introduction

The American Oystercatcher (*Haematopus palliatus*) is listed as a "Species of

High Concern" by the U.S. Shorebird Conservation Plan due to its low population size of

ca. 10,000 and of these only 3,000 individuals are likely breeding adults (Brown et al.

2001). Studies of American Oystercatcher productivity along the Atlantic Coast have

found that reproductive success is often quite low with productivity estimates commonly

< 0.25 fledglings per pair (Davis et al. 2001, McGowan et al. 2005, Nol 1989). While

there is evidence of range expansion in the northeast, American Oystercatcher population

estimates indicate a decline in the mid-Atlantic (Mawhinney et al. 1999; Davis et al.

2001). Threats from coastal development, recreational disturbance, elevated predation

rates associated with human activity, and climate change may result in a future

population decline for this long lived species. Range-wide measurements of annual

fecundity and identification of reasons for failure are needed in order to design strategies

for increasing reproductive success and setting conservation goals for this species.

South Carolina supports *ca*. 400 breeding pairs of American Oystercatchers, the

majority (*ca*. 230 pairs) of which nest within the Cape Romain Region (Sanders et al.

2008). The Region also serves as an important site for the population during the non-

breeding season with *ca*.1900 wintering oystercatchers (Sanders et al 2004). This area

provides nesting and foraging habitat for this species and preliminary data suggest that

reproductive success varies widely among habitat types in the Region. Oystercatchers in

this Region nest primarily on mounds of washed oyster shells along the Atlantic Intracoastal Waterway (hereafter AICW). Although productivity has not been quantitatively measured along the AICW, it appears to be low (SCDNR unpublished data). Disturbance from boat traffic, storm overwash and predation of nests by mainland predators are suspected causes of nest failure along the AICW. In contrast, oystercatchers that nest in Bulls Bay, which is farther from the mainland and relatively devoid of boat traffic during the nesting season, are predicted to have higher rates of reproductive success. To date, quantitative data for reproductive success and reasons for failure are not available, but are needed to ascertain how the Cape Romain Region is contributing to the larger Atlantic population. By quantifying rates of nest loss and chick loss, and by determining which factors are contributing to nest failure between and among nesting sites this study may offer insight into the population decline of American Oystercatchers within this core breeding range.

The goal of this study was to examine reproductive success of American Oystercatchers in the Cape Romain Region and to identify factors associated with nest loss. The study focused on two areas within the Cape Romain Region, the AICW and Bulls Bay. My objectives were to (1) measure and compare nest survival including hatching success and productivity of American Oystercatchers between these two locations, (2) determine causes and timing of nest failure with a focus on overwash and predation events, and (3) measure the frequency, timing and factors affecting re-nesting.

Methods

Study Area

The Cape Romain Region (Fig. 2.1) is comprised of barrier islands, shallow bays, tidal creeks, salt marsh (dominated by *Spartina alternaflora)*, mudflats and oyster (*Crassostrea virginica*) reefs. Elevated mounds of oyster and clam (*Mercenaria sp*.) shells formed by wind and wave energy accrete along sections of bays, estuarine islands and AICW within this region to form shell mounds. These shell mounds provide nesting habitat for the majority of oystercatchers breeding in South Carolina. I monitored oystercatcher nests on shell mounds in two study areas during the breeding seasons of 2006 and 2007: along the AICW adjacent to Cape Romain National Wildlife Refuge (CRNWR) and in the southwestern section of Bulls Bay within CRNWR (Fig. 2.1). Bulls Bay is a shallow bay within the CRNWR and is separated from the mainland by extensive *Spartina* salt marsh. Shell mounds within Bulls Bay accrete along the salt marsh edges from the accumulation of washed oyster shells deposited by winter storms. The AICW is a navigable waterway established for commercial and recreational boat traffic and passes through the Cape Romain Region. In contrast to Bulls Bay, shell mounds along the AICW are formed by waves from boat wakes. Sections of the AICW are adjacent to the mainland and several boat ramps within this Region provide access for recreational vessels. Boat wakes from large watercraft can create large waves that can wash over shell mounds along the AICW during high tides.

Nest Monitoring

Nest searching and monitoring occurred from late March until *ca*. mid-July during 2006 and 2007 in both study areas. I searched for active oystercatcher nests on all shell mounds along the AICW from marker 67 to marker 96, (*ca.* 12.6 km) and along the southwestern edge of Bulls Bay from Venning Creek to the Bull Island Channel (Figure 2.1). Because oystercatchers are conspicuous and vocal when territorial, I was confident that on days I searched for nests, I located nests for every active pair within the study area, however, nests may have been initiated and lost between nest-checks. Once a nest was discovered a 12 cm nail was anchored into the shell mound nearby as a marker. The location was recorded (± 3 m) using a handheld GPS, the number of eggs present in each nest was recorded, and the band combinations of any adults observed at the nesting territory also were recorded. To assess the possibility that flooding may have affected nests, I buried plastic cups (350 ml) near each nest. These wash-over cups were oriented horizontal to and parallel with the nest bowl and contained holes along the edge that allowed salt water to collect in the bottom of the cup if flooding occurred. The wash-over cups had lids to prevent rainwater from entering the cup.

Nests were then monitored at *ca.* 3 d intervals until the eggs hatched or until the nest failed. If a nest failed before hatching, I attempted to determine the cause of failure. I searched the area for signs of predators (e. g. scat, tracks) or other disturbance (e. g. digging, broken eggs) to the nest. If a wash-over cup contained saltwater, was dislodged from the shell mound, or if wrack debris accumulated at the nest site since the previous nest-check, then I attributed nest loss to an over-wash event.

I measured the frequency of re-nesting in American Oystercatchers and sought to determine the factors that were most strongly related to the time between re-nesting events. American Oystercatchers are typically monogamous (Nol and Humphrey 1994) and show strong nest site fidelity (Nol 1989). In addition, the majority of nesting pairs (72% in 2006, 78% in 2007) in this study had at least one banded adult identifiable by unique color combinations. Therefore I assumed the same pairs were making additional nesting attempts when re-nesting occurred on the same shell mound. When multiple nesting attempts occurred at the same site (i.e., for the same pair), I used a general linear model with manual backward selection to assess the relationship between the number of days between the loss of a clutch and the laying of a replacement clutch (i.e., interclutch interval) and a suite of independent variables: study area, year, eventual fate of the replacement clutch, re-nest classification (defined as a categorical variable such that "B" nest attempts following "A" failure = AB, "C" nest attempts following "B" failure = BC) and interaction terms of re-nest classification*location and re-nest classification*year. The interclutch interval of third and forth re-nest attempts (i.e., CD classification) was not used in this model because there were no data for this nesting interval in Bulls Bay in 2006. Terms with $P > 0.10$ were deleted at each step of the backward selection process until only terms with $P \leq 0.10$ remained. The number of days of interclutch intervals was square-root transformed, and means are reported as raw values $\pm$ 1 standard error.

A multinomial logistic regression (PROC LOGISITC, SAS) was used to determine the odds of a clutch size increasing from one to two eggs or from two to three or more eggs. Independent variables included location, year, nest attempt, nest fate or chick fate.

Nest Success and Statistical Analyses

Daily survival rates were calculated using the Mayfield method (Mayfield 1961) and Mayfield logistic regression (Hazler 2004). Nesting success for the Mayfield method is defined as survival of any of the nest contents, and partial clutch losses are ignored. Failed nests were designated as lost at the midway point between nest checks (Mayfield 1961). The Mayfield method assumes that daily survival is constant during the incubation stage and constant during chick rearing. Separate daily survival rates were therefore calculated for the incubation and chick rearing stages as:

daily survival rate = 1 - (losses/exposure days)

where losses were the number of nests lost during the incubation stage or during the chick rearing stage, and exposure days were the total number of days the nest or chicks were under observation. The probability of survival for an entire stage (i.e., incubation or chick rearing) was then calculated as the survival rate raised to an exponent equal to the number of days in that stage (i.e., 27 d for incubation and 35 d for fledging for American Oystercatchers; Nol and Humphrey 1994). When survival rates differed between stages within a location-year (e.g. within Bulls Bay in 2006) the probabilities of each stage were multiplied together (Johnson 1979) to obtain the probability of a nest surviving from incubation through fledging. When the daily survival rates did not differ between stages, the data were pooled and the survival rate was raised to the sum of the duration of the incubation stage plus the chick rearing stage. Differences in survival rates between the incubation and chick rearing stages were assessed by calculating Z statistics (Johnson 1979). Differences in survival rates within stages between years and within stages between locations were also assessed by calculating Z statistics. Standard errors were

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calculated according to Johnson (1979) and confidence intervals were calculated according to Hensler and Nichols (1981).

Mayfield logistic regression was used to estimate daily nest survival during incubation only and to examine the relationship between survival during this stage and a suite of explanatory variables. Mayfield logistic regression extends the traditional Mayfield estimate and incorporates explanatory variables in a logistic regression framework. Variables included in the model were year, location, a midpoint term (midpoint of the number of days of the nesting interval relative to the entire season), midpoint squared, and all 2-way interactions. I followed procedures described by Hazler (2004) and Corcoran et al. (2007). I first assessed goodness-of-fit of the global model with the Hosmer and Lemeshow (2000) goodness-of-fit test and estimated over-dispersion ($\hat{c}$ = variance inflation factor) by dividing deviance by the degrees of freedom from the global model. Standard errors for subsequent models were adjusted by this factor. All calculations were performed using the LOGISTIC procedure in SAS (SAS Institute Cary, NC). I reported odds ratios and their 95% confidence intervals. I reported the predicted survival based on the explanatory variables as:

$$\hat{S} = \{1 + \exp(-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n))^{-1}\}$$

where $\hat{S}$ = daily survival rate (DSR), β_0 was the model intercept, β_i were parameter estimates, and X_i were measured covariates. The probability of nest success was calculated by raising the daily survival rate to an exponent equal to the number of days during incubation (27 d). Sample sizes during chick rearing were inadequate to allow for the use of Mayfield logistic regression.

Productivity of oystercatchers also was calculated using the "apparent nest success" method. Although apparent nest success often overestimates survival because it disregards the stage of the nesting cycle when the nest was found, or the possibility that nests may have been initiated and failed before detection (Mayfield 1961), it is included here to allow for comparisons with other studies. Hatching success (% nests hatching $\geq$ 1 egg) and fledging success (% chicks to reach 35 days) were each calculated as a percentage of total nest attempts. Productivity was calculated as the number of chicks fledged per pair.

For all analyses I considered significance to occur when $P \leq 0.10$, although actual P-values are reported throughout. Mean and coefficient estimates are presented $\pm$ 1 standard error unless stated otherwise.

Results

Nesting Cycle

I monitored 53 breeding pairs of oystercatchers in 2006 and 46 breeding pairs in 2007 (Table 2.1). The duration of nesting activity (time from initiation of first nest until the last nest or chick failed to hatch or fledge) in 2006 and 2007 was 111 and 106 d, respectively. In 2006, nests were first found on 7 April (laid *ca.* 30 March) along the waterway and on 12 April (laid *ca.* 1 April) in Bulls Bay, and the last nests were initiated on 19 June. In 2007 nests were first found on 4 April (laid *ca*. 30 March) along the waterway and 10 April (laid *ca* 5 April) in Bulls Bay, and the last nest was initiated on 22 June.

Replacement clutches were common. In 2006 (Figure 2.2), 53 pairs made 95 nest attempts, and in 2007 (Figure 2.3) 46 pairs made 105 nest attempts. In 2007 hatching

success (hatched $\geq$ 1 egg) was higher for subsequent attempts, however in 2006 hatching success was more variable among attempts (Figure 2.4). The interclutch interval (time between nest failure and the laying of a replacement clutch) ranged from 6 to 53 days. The majority of re-nests were made within two weeks of nest loss (i.e., 70% of the observations were within 14 days). Re-nest classification, year, and location best predicted the interclutch interval ($F_{3, 1} = 4.29$ $P = 0.007$, $r^2 = 0.12$). The mean number of days between loss of the first nest and initiation of the second nest (16.9 ± 1.2) was greater ($P = 0.03$) compared to the interval between the loss of the second nest and initiation of the third nest (12.9 ± 0.8). There were trends ($F_{3, 1} = 3.2$, $P = 0.08$) towards longer re-nesting intervals in 2006 (18.0 ± 1.7 days) compared to 2007 (14.0 ± 0.9 days) and longer re-nesting intervals ($F_{3, 1} = 3.5$, $P = 0.06$) along the waterway (16.7 ± 1.1 days) compared to Bulls Bay (12.8 days ± 1.3 days).

The mean clutch size pooled among all nesting attempts was 2.42 ± 0.06 (n = 200, range 1 to 6). Neither location ($\chi^2_1 = 0.87$, $P = 0.35$) nor year ($\chi^2_1 = 0.11$, $P = 0.74$) were significant in predicting clutch size. The odds of the clutch size changing did vary, however, with nest attempt ($\chi^2_3 = 10.6$, $P = 0.01$). First nest attempts were 12 x more likely to have a larger clutch compared to fourth attempts ($P = 0.02$). No such differences were observed for other intervals (P > 0.19 for each).

Apparent Success

In 2006, 24 nests (25%) hatched $\geq$ 1 egg while in 2007 six nests (6%) hatched $\geq$ 1 egg. The hatching success per pair for 2006 and 2007 was 45% and 13%, respectively. The hatching success per nesting attempt for both years combined was 15%. Oystercatchers fledged 23 chicks in 2006 (24%) and two chicks in 2007 (2%) across both study areas (Table 2.1).

Daily Survival

Mayfield estimates of daily survival during the incubation stage and during the chick rearing stage are presented in Figure 2.5. Results from the Mayfield logistic regression model indicated that the global model which included terms for year, location, midpoint, midpoint^2, and all 2-way interactions fit the observed survival data from the incubation stage well ($\chi_8^2 = 10.1$, $P = 0.26$). The estimated c-hat based on the global model was 1.5269 and I used the square root of c-hat to adjust all models (Allison 1999, Corcoran et al. 2007). Based on the intercept-only model (i.e., constant model) the daily survival rate for oystercatcher nests during incubation from both years and study sites was 0.934 (95% CI: 0.929-0.939), corresponding to a nest success of 16%. There was a positive relationship between daily nest survival and the midpoint of the nesting cycle (0.01 ± 0.005, $\chi_1^2 = 4.2$, $P = 0.02$) whereby for every one day increase in midpoint the odds of a nest surviving one day were predicted to increase 1.011 times (95% CI: 1.001-1.02), all else being equal (Figure 2.6).

The final model also included a significant term for year*location (0.23 ± 0.12, $\chi_1^2 = 3.4$, $P = 0.06$). In 2006, there was a higher probability of success ($Z = 2.4$, $P =$

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0.008) for nests located in Bulls Bay (0.966, 95% CI: 0.949 - 0.984) compared to nests on the AICW (0.938, 95% CI: 0.922 - 0.954). Daily survival rates were poor in 2007 (0.903, 95% CI: 0.880 - 0.926 for AICW; 0.895, 95% CI: 0.862 - 0.927 for Bulls Bay) and there was no significant difference between locations ($Z = 0.41$, $P = 0.34$). Within both Bulls Bay and the AICW, the probability of nest success during incubation was greater in 2006 (AICW $Z = 2.4$ $P = 0.007$, Bulls Bay $Z = 3.8$, $P = \leq 0.0001$) compared to 2007 (Figure 2.5).

Based on a fledge date of 35 days post-hatch, Mayfield estimates of daily survival during the chick rearing stage were calculated for each study site and year. In 2006, Bulls Bay had a significantly higher ($Z = 1.87$, $P = 0.03$) daily survival estimate during chick rearing (0.991, 95% CI: 0.980 - 1.00) compared to the AICW (0.967, 95% CI: 0.944 - 0.989). However, in 2007, only 4 chicks survived to estimate chick rearing on the waterway, and although this was a small sample size, this estimate (0.983, 95% CI: 0.961-1.00) was similar to chick rearing estimates in 2006 for both the AICW (Z score = 1.01, $P = 0.14$) and Bulls Bay (Z score = 0.56, $P = 0.29$). No chicks survived in Bulls Bay in 2007.

There were differences in daily survival between the incubation stage and the chick rearing stage for nests along the AICW in 2006 ($Z = 2.05$, $P = 0.02$), along the AICW in 2007 ($Z = 4.38$, $P \leq 0.0001$), and in Bulls Bay in 2006 ($Z = 2.34$, $P = 0.009$). The probability of success from incubation through fledging was 29% in 2006 for Bulls Bay, 5% in 2006 along the AICW, < 1% in 2007 for Bulls Bay, and 3% in 2007 along the AICW.

Nest Fate and Chick Loss

Of the 200 attempts recorded in both study areas in both years, 85 % of nests (n = 170) failed before hatching. The major identifiable cause of nest loss in both years and in both locations was overwash of nests (Figure 2.7). Nests also were lost frequently to predation, primarily avian, and nests along the AICW appeared to be depredated more frequently compared to those in Bulls Bay (Figure 2.7). For most chicks I was able to determine the timing of failure and the approximate age of the chicks when they died. The majority of chicks perished early (within 20 days of hatching) and chicks expired more frequently on the waterway (Table 2.2). Because oystercatcher chicks are precocial and mobile within hours after hatching (Nol & Humphrey 1994) they are difficult to locate and therefore causes of chick loss prior to fledging were difficult to determine in a majority of cases.

Discussion

Hatching success and productivity of American Oystercatchers in the Cape Romain Region of South Carolina was relatively low in both areas and years during this study. Hatching success and productivity during this study appear to be similar to values reported for other areas in the southeastern USA, although there are no comparable data on reproductive success of American Oystercatchers in South Carolina and little has been published on reproductive success elsewhere in their range. For example, the hatching success (15%) and fledging rate (0.25 chicks per pair) during this study appears similar to results reported for North Carolina (24% hatching success and 0.19 chicks fledged per pair over eight years on barrier beaches; McGowan 2004) and Virginia (14% mean hatching success and 0.24 chicks fledged per year over four years on several coastal

islands; Nol 1989). Some of the highest reproductive rates for American Oystercatchers have been reported in Georgia with 38% hatching success and 0.71 chicks fledged per pair (Sabine et al. 2006) and more recently, high hatching and fledging success (productivity > 1 chick per pair) has been observed for several years on islands on the eastern shore of Virginia (A. Wilke unpublished data). Despite reports of areas and years of high fecundity, overall rates of reproductive success in American Oystercatchers have been low (McGowan 2004; George 2002; Nol 1989; Davis et al. 2001).

Reproductive success of oystercatcher species worldwide appears to be relatively low and success often varies substantially within populations among sites and years (reviewed by Hockey 1996). This spatial and temporal variability often reflects local parameters acting on nest survival, such as rates of predation and overwash. Differences in reproductive success between years during my study were attributed primarily to the tropical storms of 2007 which caused catastrophic flooding of nests across both locations. Similarly, Nol (1989) found that annual reproductive success of oystercatchers on barrier islands in Virginia varied both among multiple pairs and within particular pairs during a three year study. In my study, reproductive success also varied between study areas with higher success often achieved within Bulls Bay compared to the waterway. Spatial differences in reproductive success within populations appear to be common in the southeastern USA. For example, reproductive success in North Carolina differed within a region between pairs nesting on river islands and those nesting on barrier beach habitat (McGowan et al. 2005) and in Georgia, reproductive success differed between the northern and southern portions of one barrier island (Sabine et al. 2006). While reproduction in American Oystercatchers varies between sites and among years, it is still

unknown if these low levels of annual productivity are adequate to maintain the population (Davis 1999).

Nest Fate

Apparent nest success often overestimates survival because successful nests have a higher rate of detection than failed nests (Johnson & Shaffer 1990), however, apparent nest success was similar to Mayfield estimates for this study. This may be because of the frequency of nest searches and the visibility of oystercatcher nests on shell rakes. Oystercatcher nests were easily located at my study locations and 3 day intervals of nest checks appeared to be adequate to estimate hatching success using the apparent nest success method. Nests were found as they were laid and unsuccessful nests were accounted for with the same frequency as successful nests. Because of higher detection of nests, the apparent nest success estimate may not have overestimated hatching success therefore yielding similar results as the Mayfield method.

Hatching success, nest survival and productivity were all higher in Bulls Bay compared to the waterway. Differences in breeding success between sites appeared to be due to differences in the rates of overwash in the two study areas, although levels of predation or quality and location of foraging territories also may have differed between the two areas. The role that each of these factors may play is discussed in turn.

Overwash was the most frequently identified cause of nest loss in both study areas. The majority of overwash events in both years were associated with storms and extreme high tides, including two tropical storms that occurred during May and June of 2007. It appears that nests in the Cape Romain Region are prone to overwash events due

in part to the physical structure of the shell mound habitat. For example, during spring flood tides only the top portion of shell mounds are exposed. If high tides are accompanied by storms and wind driven waves, these shell mounds in all areas of the Cape Romain Region can be severely reduced, leveled, or submerged. The prevalence and timing of overwash due to spring tidal flooding also may be the primary factor underlying the trend I observed towards higher nesting success later in the breeding season. In the Cape Romain Region, the highest tidal periods occur in April and May which coincides with oystercatcher nest establishment. For example, ca. 80% of first nesting attempts failed in both study areas during the two years and the majority were lost to overwash events that appeared to be due to tidal or storm flooding. Similarly, hatching success for first nests in Pied Oystercatchers (*Haematopus longirostris)* in Tasmania was significantly lower at sites that were more exposed to wind-driven tidal flooding compared to nests at other sites (Lauro & Nol 1993). For pairs that continually failed in Virginia, nest loss also occurred primarily from high water during spring tides (Nol 1989). The effect of high spring tides can be exacerbated by boat wakes especially along the waterway where boat traffic can be frequent and where the intensity of the wakes can be severe. American Oystercatchers demonstrate nest site fidelity and birds in the Cape Romain Region that lost nests continually re-nested at the same spot on a shell mound even if the nest elevation was prone to flooding.

Predation of nests during the incubation stage is also a major factor affecting nest survival for oystercatcher species worldwide (Hockey 1996). For example, in North Carolina mammalian predators, specifically raccoons (*Procyon lotor*), were frequent predators of nests on barrier islands (McGowan 2004), and in Georgia predators

including bobcat (*Lynx rufus*) and raccoon were responsible for the majority of nest loss in one area of Cumberland Island National Seashore (Sabine et al. 2006). In my study area, mammalian predation was rarely documented as a cause of nest failure. A small number of oystercatcher pairs nested on the mainland side of the waterway, however the majority of pairs, (*ca*. 77%) nested on the opposite side from the mainland. Pairs may make nests here to avoid mammalian predators. This may be because tidal channels and the waterway separate shell mounds from the mainland and these may be substantial barriers for potential predators like raccoons. In a pilot study in 2006, track stations were deployed on shell mounds in both study areas to assess presence of mammalian predators. In 135 nights of sampling throughout the nesting season, evidence of mammals was detected on only 5 occasions (1 set of raccoon tracks, 4 sets of rodent tracks). Evidence of raccoons has been documented infrequently along the waterway and in Bulls Bay, and only one lost nest in this study was attributed directly to raccoon. Aquatic predators, such as mink, would not be deterred by channels and hence could pose a predation risk.

Avian predation appeared to be much more prevalent during my study and egg loss due to avian predation was likely responsible for some of the undetermined nest loss in this study as well. Avian predators often leave no evidence of predation, however, making positive identification difficult. Signs of avian predation, (i.e., punctured eggs), were observed more frequently on the waterway than in Bulls Bay. In a pilot study using video monitoring equipment in 2007, one flock (5-6 individuals) of American Crows (*Corvus brachyrhynchos*) was recorded puncturing and eating the eggs of an oystercatcher pair on the waterway. In another incident on the waterway, a Laughing Gull (*Larus atricilla*) was observed stealing an egg from an oystercatcher nest while the adult

was off the nest but still on the territory. Avian predation may be more prevalent on the waterway because it is adjacent to the mainland which may have the capacity to support egg predators such as Crows.

In the 200 nesting attempts monitored during the two years of this study, only 25 chicks fledged and over 50% of these fledged from Bulls Bay although only 34% of pairs monitored for this study nested in Bulls Bay. Differences in fledging success between Bulls Bay and the waterway may be attributed to differences in provisioning and adult attendance patterns between these areas (See Chapter Three). For example, I observed that pairs nesting along the waterway did not forage at the nesting site as frequently as pairs nesting in Bulls Bay. Often on the waterway one parent would leave the territory while the other remained on the territory, however, in Bulls Bay both parents were usually present at the nesting territory while foraging. This foraging pattern resulted in a slightly lower rate of parental attendance along the waterway which subsequently may have affected chick survival. It is also possible that the frequency of feeding was not as great along the waterway and this also may negatively affect chick growth and survival. Studies examining the reproductive success of European Oystercatchers (*Haematopus ostralegus*) found that birds that had contiguous nesting and feeding areas had higher fledging success than those of "leapfrog" pairs that commute to feeding territories (Ens et al. 1992). The reduced survival of chicks from 'leapfrog' territories was attributed to increased rates of starvation which in turn was likely due to insufficient meal delivery rates. Food transport cost of the parents was also suspected to be higher in leapfrog territories. Nol (1989) also found a positive correlation between size of nearby foraging areas and fledging success for American Oystercatchers nesting in Virginia where parents

feeding on large and nearby foraging territories raised more chicks than those with small

or no nearby foraging territory. However, she attributed the relationship of feeding

territory size and fledging success to the high visibility of the feeding territory which

allowed parents to be vigilant for predators. Similarly, along the waterway oystercatchers

that commute to forage may leave chicks unattended and vulnerable to predation; in

contrast, parents in Bulls Bay may be able to forage at the nest site and defend chicks

from predators.

Multiple Clutches

Replacement clutches for oystercatchers are common (Nol & Humphrey 1994)

but attributes of re-nesting such as interclutch intervals and subsequent clutch sizes have

not been examined in detail. Frequent nest checks most likely resulted in high

detectability of replacement clutches for this study and hence provided me an opportunity

to examine parameters of re-nesting including replacement clutch size, and duration of

interclutch intervals.

Nest loss occurred throughout each breeding season. In two years, 67% of pairs

laid second nests and 35% laid three or four nests. Clutch sizes were similar among first,

second and third nesting attempts suggesting that the resources available to

oystercatchers nesting within the Cape Romain Region are numerous or of high quality

and hence enable oystercatchers to continually invest energy into reproduction. Although

no direct measure of foraging resources have been examined in this area during the

breeding season, South Carolina does support *ca*. 30% of the Atlantic Coast population of

American Oystercatchers during the winter and large flocks of wintering birds roost in

the Cape Romain Region (Sanders et al. 2004). Sundar (2006) found a positive association of wetland size and flock size in Asian Openbills (*Anastomus oscitans*), a wading bird that forages on mollusks and implied that food availability may be an important factor affecting flock size of this species in India. If winter flock sizes of American Oystercatchers are an indication of food quality or availability for the Cape Romain Region, then this area may provide quality foraging resources during the breeding season also.

The length of interclutch intervals observed in this study may be related to a variety of factors: time left in the breeding season, the stage of the nest (i.e., during the egg laying stage or incubation stage), or the differences in rates of disturbance between nesting locations. For example, re-nest intervals in Dusky Canada Geese (*Branta canadensis occidentalis*) decreased as the nesting season advanced (Fondell et al. 2006). In my study it appears that shorter interclutch intervals in 2007 compared to 2006 were due to the timing of tropical storms in 2007. Tropical storm Andrea made landfall on the central coast of South Carolina in early May as did tropical storm Barry in early June. Pairs that lost nests due to flooding from these storms in May and June experienced a shortened remainder of the nesting season, and this shortened season may have influenced oystercatchers to re-lay at shorter intervals. As date advances the time available to successfully fledge a chick decreases, therefore pairs would need to reduce the time between re-nests in order to have a successful breeding attempt. Likewise, interclutch intervals were shorter for subsequent nesting attempts initiated later in the season (BC interval vs. AB interval).

Interclutch intervals were shorter in Bulls Bay compared to the waterway. Length of the interclutch interval may be a factor of the stage of the nest when the loss occurred (i.e., egg laying stage vs. incubation stage). For example, for American Coots (*Fulica americana*) (Arnold 1993) and for BrÜnnich's Guillemots (*Uria lomvia*) (Hipfner et al. 1999) re-laying intervals were longer in pairs that lost clutches during the incubation stage than those that lost clutches during egg laying. This difference is most likely attributed to follicle development in which females that lose eggs during the laying stage may have the ability to produce eggs sooner than those females that had begun incubating (Arnold 1993). On the waterway, nests that were lost were older than nests that were lost in Bulls Bay, and pairs therefore, had been incubating for a longer duration on the waterway than pairs in Bulls Bay. Likewise, pairs nesting in Bulls Bay may have still been in the egg laying stage when nests were lost. If oystercatcher females demonstrate similar physiological capacity as coots and guillemots, females in Bulls Bay which lost nests earlier in their cycle may have had the ability to form eggs sooner and thus re-nest at a faster rate than females on the waterway.

Different rates of disturbance may have contributed to the differences I observed in the duration of interclutch intervals. Pairs on the waterway may incur a greater level of disturbance from human activity than pairs nesting in Bulls Bay. In several incidences during this study, human activity was observed directly disrupting nesting birds on the AICW including fishing from shell mounds within several meters of nests and destruction of eggs by children. No such disturbances were detected in Bulls Bay.

Management Implications

Overwash is a major cause of oystercatcher nest loss on shell mounds in the Cape Romain Region. While some studies have experimented with elevating nest sites to avoid flooding (Nol & Humphrey 1994), elevating shell mounds in the Cape Romain Region would require continual maintenance to prevent wind and wave erosion and is probably not an effective long-term management tool. Elevating nest sites may draw attention to nests, especially from avian predators such as crows which may cue on altered features of the habitat. Avian predation already appears to be a frequent source of nest loss in this Region. While studies in Virginia and North Carolina have shown increases in oystercatcher productivity where mammalian predators are controlled, this management tool is labor intensive, and control of avian predators is probably not feasible in the Cape Romain Region. Funds may be better spent on identifying and protecting areas of high reproductive success. Nesting success and chick survival may be related to foraging resources in the area. Connecting fecundity with foraging would provide managers with the information of where to target habitat protection and, if needed, enhancement. Accurately estimating survival rates is important for understanding American Oystercatcher population dynamics. While fledging success is the metric to determine productivity, on several occasions I did not observe chicks after their fledge date suggesting that mortality occurs after 35 days post hatch. Further study on chick survival is needed to accurately estimate fecundity and provide information of the sources of chick mortality and other habitat related factors that affect survival during this stage.

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Table 2.1 Reproductive success of American Oystercatchers within the Cape Romain Region, South Carolina, April-July 2006 & 2007.

	No. pairs	No. nest attempts	Exposure days	Number of failures	No. clutches that hatched (%)	No. fledglings (%)	Productivity estimate[1]
Waterway							
2006	35	71	919.5	57	14 (20)	9 (13)	0.26
2007	30	67	619.0	60	4 (6)	2 (3)	0.07
Bulls Bay							
2006	18	24	418.0	14	10 (42)	14 (58)	0.78
2007	16	38	341.5	36	2 (5)	0	0
Total	99	200		167	30 (15)	25 (13)	0.25

[1]Number of young fledged/number of pairs

Table 2.2 Chick loss by age for American Oystercatchers in the Cape Romain Region, South Carolina, April – July, 2006 and 2007.

Year	Location	1-6 days	7-20 days	21-35 days	35 + days	Total
2006	Waterway	5	4	1	0	10
	Bulls Bay	0	1	1	1	3
2007	Waterway	0	1	1	2	4
	Bulls Bay	1	1	0	0	2
Total		6	7	3	3	19
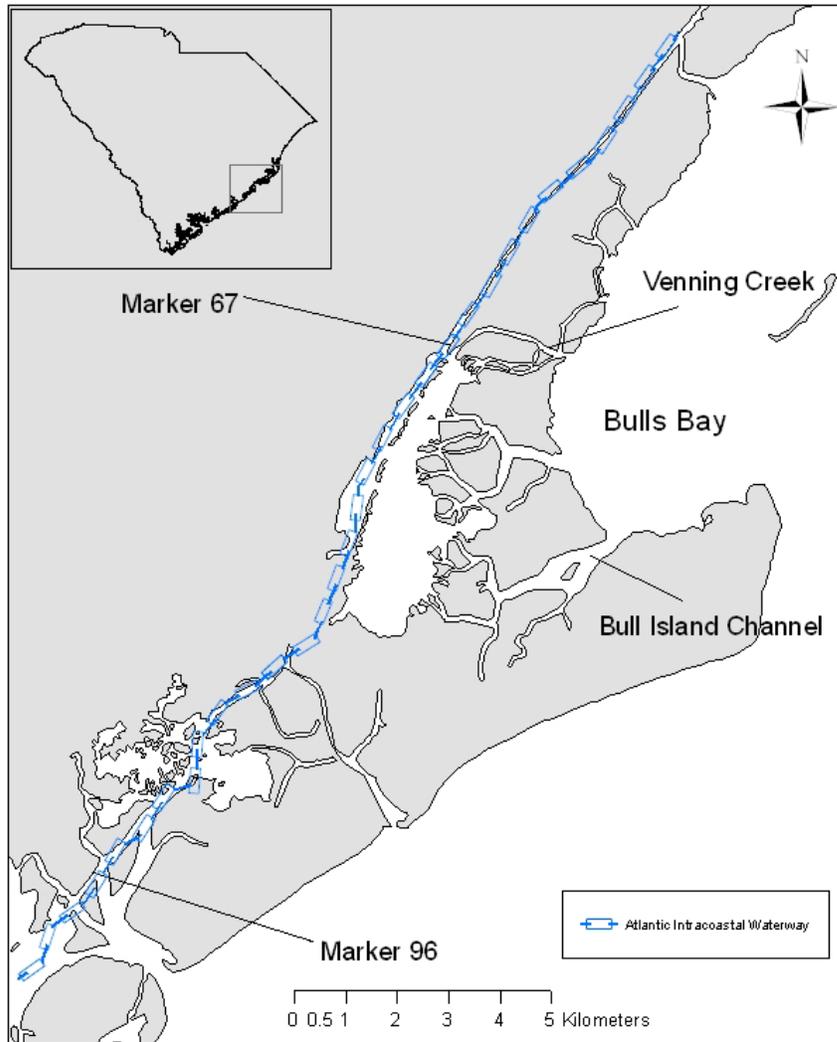
Figure 2.1 Study area within the Cape Romain Region, South Carolina. Study nests occurred along the Atlantic Intracoastal Waterway between markers 67 and 96, and in Bulls Bay between Venning Creek and the Bull Island Channel.
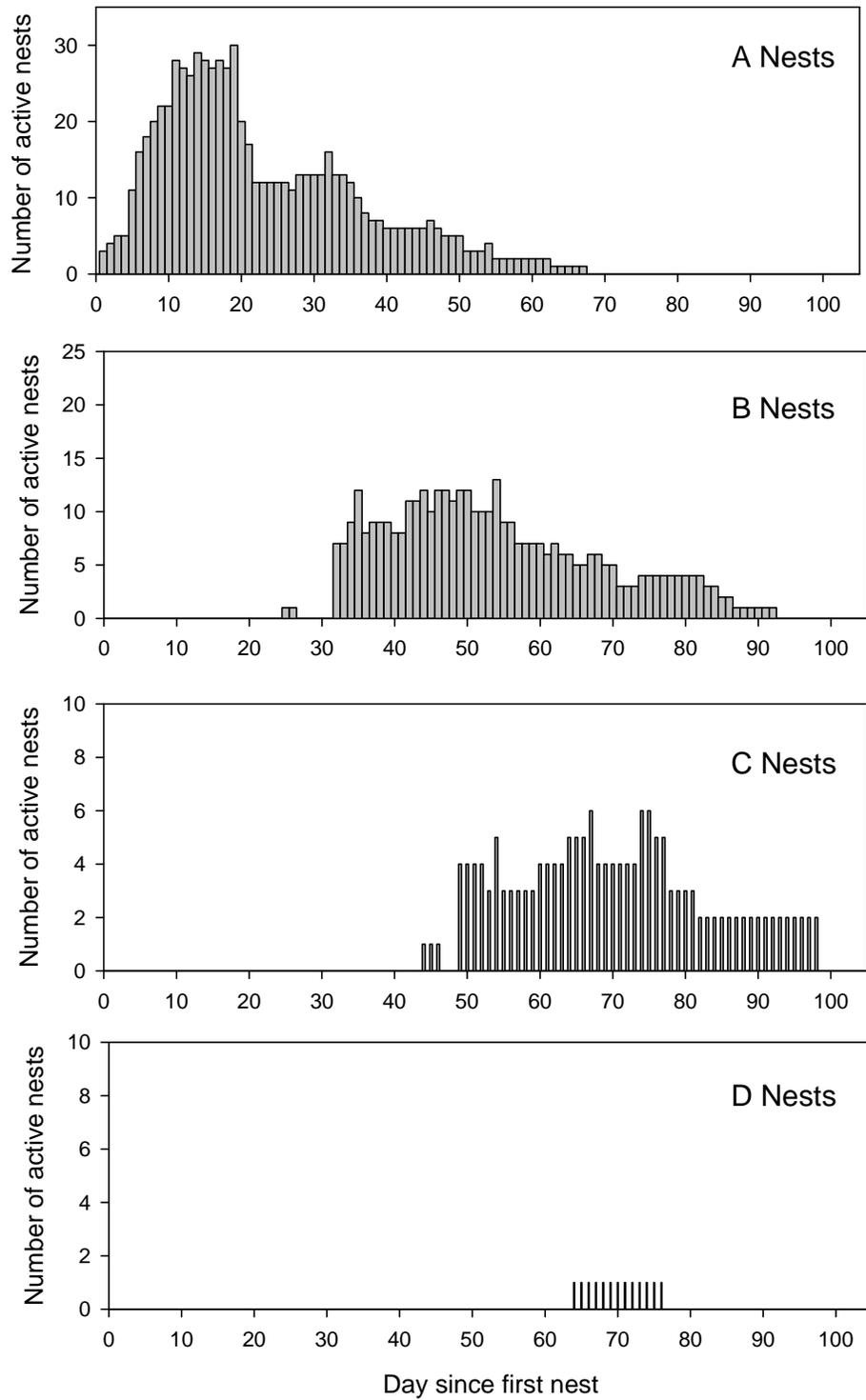
Figure 2.2 Nesting cycle of American Oystercatchers in the Cape Romain Region, South Carolina, April – July, 2006. Day 0 = 06 April 2006.
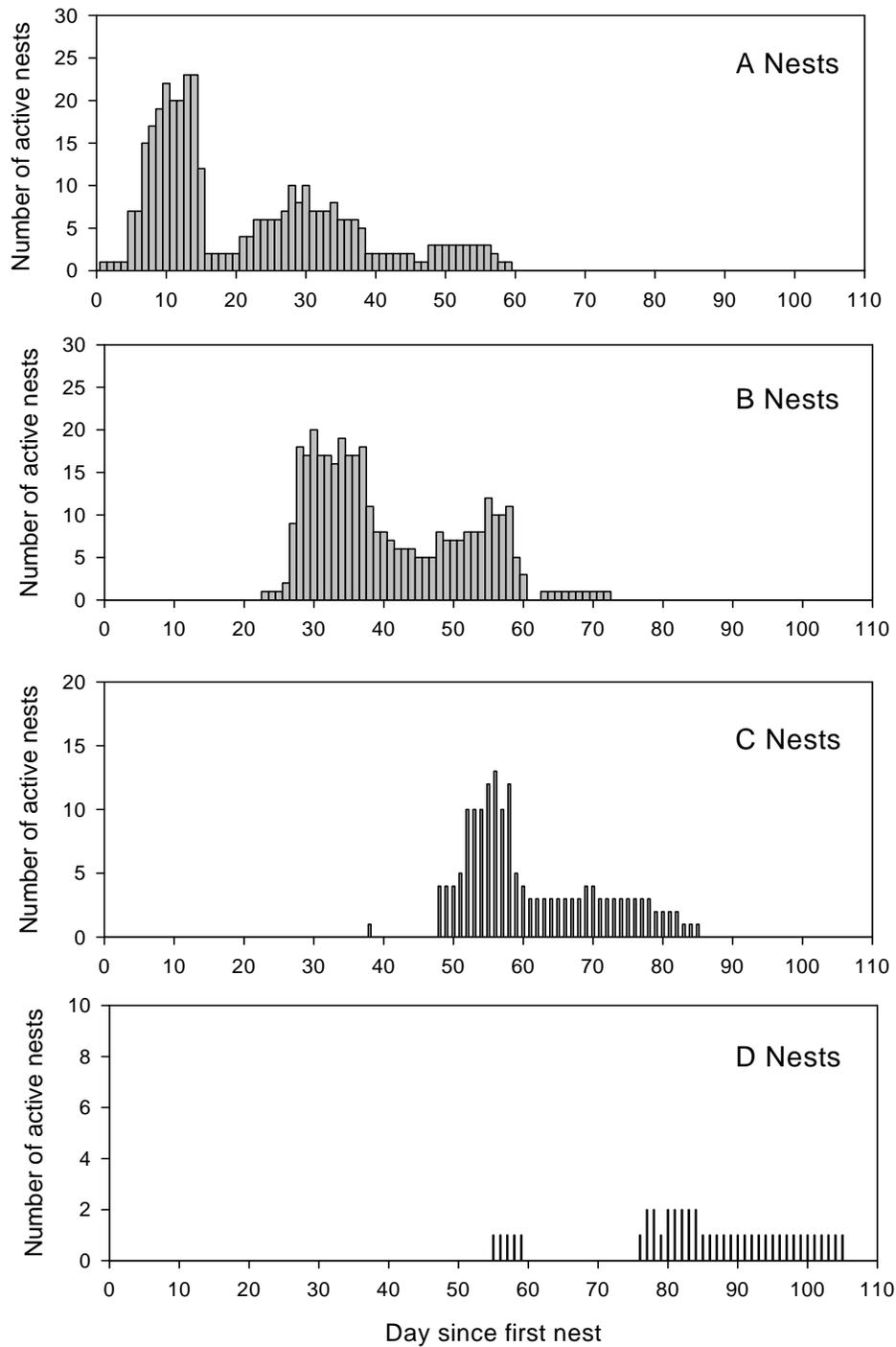
Figure 2.3 Nesting cycle of American Oystercatchers in the Cape Romain Region, South Carolina, April – July, 2007. Day 0 = 03 April 2007.
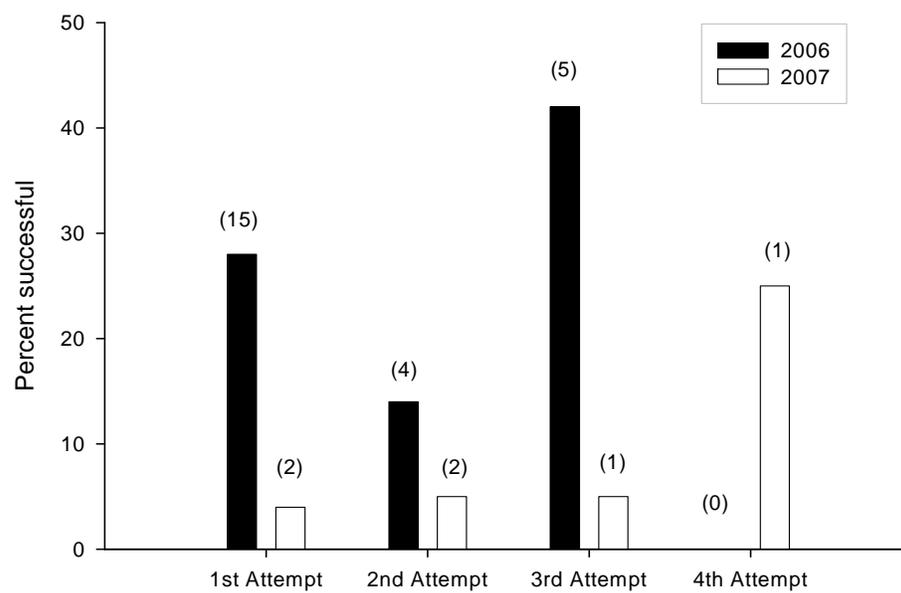
Figure 2.4 Proportions of hatching success (hatched ≥ 1 egg) for multiple nesting attempts of American Oystercatchers in the Cape Romain Region, South Carolina, April – July 2006 and 2007. Numbers above bars indicate sample sizes.
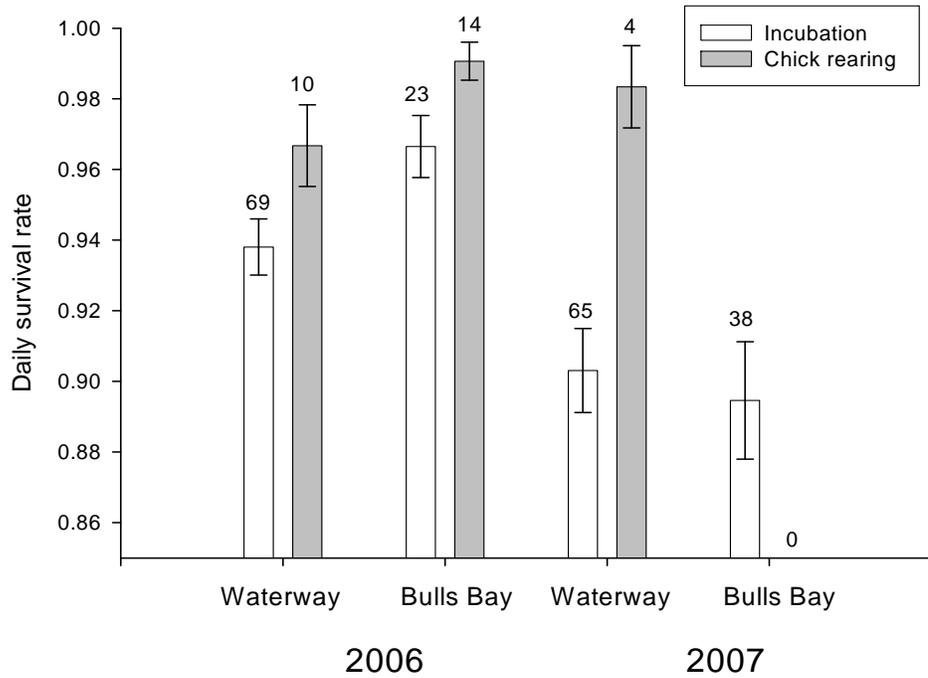
Figure 2.5 Mayfield survival estimates (± 1 SE) during the incubation and chick rearing stages for American Oystercatchers nesting in the Cape Romain Region, South Carolina, April – July 2006 and 2007. Numbers above bars indicate sample sizes. Standard errors were calculated according to Johnson (1979).
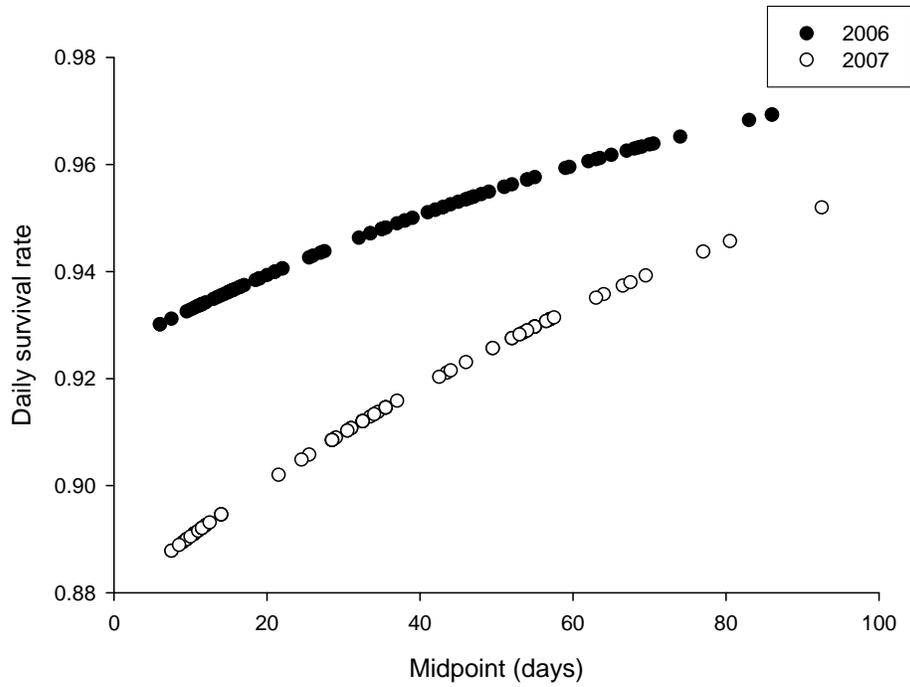
Figure 2.6 Relationship between daily survival rate of American Oystercatcher nests and midpoint of nesting interval relative to entire season in the Cape Romain Region, South Carolina, April – July, 2006 & 2007. Day 0 = 06 April 2006, day 0 = 03 April 2007.
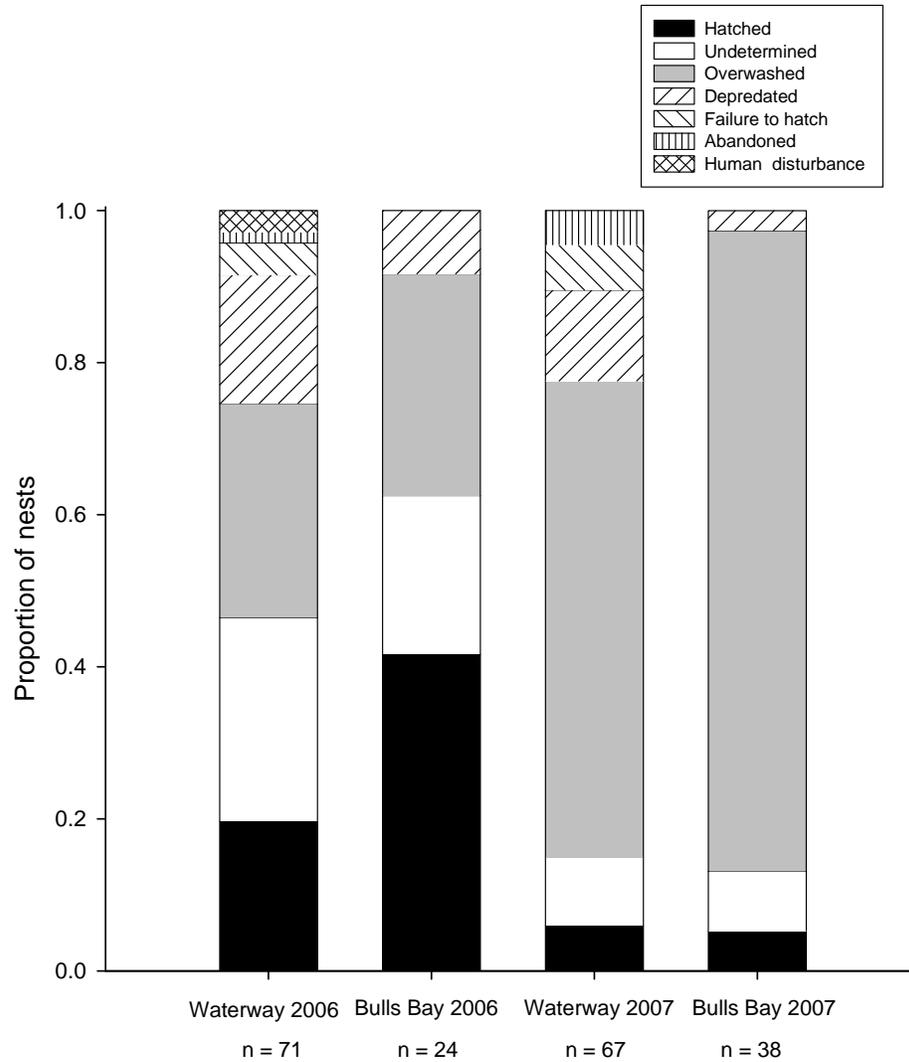
Figure 2.7 Fate of American Oystercatcher nests in Cape Romain Region, South Carolina, April – July, 2006 and 2007. n = number of nests monitored. Failure to hatch were overdue nests.

CHAPTER THREE

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

Introduction

American Oystercatchers (*Haematopus palliatus*) are listed as a species of high

concern by the U. S. Shorebird Plan (Brown et al. 2001). The current population size for

the American Oystercatcher along the Atlantic and Gulf Coasts is approximately 10,000

individuals and of those it is estimated that there are *ca*.1500 breeding pairs (Brown et al.

2005). Along with a relatively small population this species also appears to experience

low annual reproductive success due in part to predation of nests and chicks and

overwash from high tides and storm events (Nol 1989, McGowan et al. 2005 and see

Chapter 2). Other factors that affect reproductive success of American Oystercatchers

may include alteration of nesting and foraging habitat, disturbance from human activities,

or less obvious factors such as attributes of foraging territories or diet. While factors

related to foraging habitat and diet have been explored in other species of oystercatchers

(Ens et al. 1992; Bruinzeel et al. 2005) these factors have been rarely examined in

American Oystercatchers (Humphrey & Nol 1994). No formal study of oystercatcher

foraging during the breeding season has been conducted in the southeastern United

States.

The link between reproductive success and foraging ecology, specifically territory

quality, has been studied extensively in European Oystercatchers (*Haematopus*

ostralegus). Pairs defend both nesting and feeding territories and two different territory

types have been described in relation to distance between feeding and nesting sites.

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European oystercatcher pairs nesting along the edges of mudflats have contiguous nesting and feeding areas and are categorized as residents. Those pairs that nest further inland and commute to feeding territories are described as leapfrog birds (Ens et al.1992). In a study of reproductive success of European Oystercatchers, resident birds experienced higher fledging success than leapfrog parents. Reduced survival of leapfrog chicks was attributed to increased rates of starvation of chicks likely due to insufficient meal delivery rates. Food transport cost of the commuting parents was also suspected to be higher in leapfrog territories.

Two areas occupied by nesting American oystercatchers, located in the Cape Romain Region of South Carolina, may function similarly to resident and leapfrog territories. In the Cape Romain Region the majority of oystercatchers nest on elevated shell mounds and feed in extensive mudflats and oyster reefs exposed during low tides. Shell mounds form naturally by winter storms along edges of bays and estuarine islands. Oystercatchers nesting here have contiguous feeding and nesting territories and may function similar to resident pairs. In contrast, shell mounds along the Atlantic Intracoastal Waterway (AICW) are formed by waves from boat wakes and preliminary observations suggest that oystercatchers nesting here must commute to nearby oyster reefs to forage. These commuting birds may experience similar reproductive success as leapfrog birds of Europe. Linking foraging ecology with reproductive success, including chick survival, is important in understanding factors contributing to low reproductive rates and will assist in designing management strategies and setting conservation goals for this species.

South Carolina's Charleston County supports over 109 km^2 of oyster reefs within its coastal wetlands including part of the Cape Romain Region (Kinsey 2007). Sewee Bay

is a shallow bay and is a primary foraging site for large flocks of wintering oystercatchers (F. Sanders, pers. com.) and is devoid of elevated shell mounds that could be used by nesting birds. In contrast, Bulls Bay, located in Cape Romain NWR, is both a foraging and nesting location for oystercatchers. The Cape Romain Region supports the majority of South Carolina's breeding oystercatchers, and this setting provides an opportunity to examine oystercatcher foraging behavior and diet during a time of year in which it may primarily affect the fecundity of the species. Examining foraging ecology including prey choice and feeding efficiency in these two primary foraging locations will elucidate differences between sites used for foraging and nesting and those used only as foraging territories.

The purpose of my study was twofold. In 2006, I monitored oystercatcher nest success on shell mounds along the AICW and in the southwestern section of Bulls Bay, both within the Cape Romain Region. I compared the percentage of time that parents were absent from nesting territories in these locations during foraging periods and related that time to reproductive success. In 2007, I evaluated components of foraging oystercatchers at two primary oyster reefs within the Cape Romain Region. I compared the foraging efficiency and prey selection of oystercatchers foraging in Sewee Bay, a site without adjacent nesting substrate with oystercatchers foraging in Bulls Bay, where birds nest adjacent to oyster reefs.

<div align="center">Methods</div>

Use of Nesting Territories for Foraging (2006)

Oystercatcher nests were monitored and parents observed in two study areas within the Cape Romain Region of South Carolina (32º 49'-33º 05' N, 79º 20'-79º 45'

W; Fig. 3.1) from April to July, 2006. The first study area was a section of the (AICW) from marker 67 to marker 96. The second study area included the southwestern section of Bulls Bay from Venning Creek to the Bull Island Channel. Nest searching began prior to and during the egg laying stage. Nests, pairs and chicks were then monitored throughout the breeding season. Apparent hatching success (number of eggs hatched per breeding pair), fledging success (percent of chicks to reach 35 days), and productivity (number of chicks that fledge per breeding pair) were estimated in each study location. I recorded band combinations of previously banded adults and also banded additional adults and chicks in the study locations. During this study, 72% of nesting pairs were identifiable by band combination.

I conducted hour long observations of nesting pairs during the chick-rearing stage in both study locations from 18 May to 20 July 2006. Oystercatchers forage when shellfish reefs are exposed, therefore, observations were conducted either within the 2 hour period prior to or following low tide (Tidelog Southeastern Edition, Pacific Publishers, 2006). Nests within both study areas were numbered and observations were conducted on a rotating basis with additional nests added to the rotation as nests hatched. Some pairs were observed multiple times during the chick rearing stage. Observations were conducted using a spotting scope or binoculars either from land or boat, but in all cases distant enough to limit disturbance (*ca*. 50 -100 m) but close enough to observe chicks and adults. The nest site was under continuous observation during the 1 hour period. At the start of the observation period I noted the number of adults and chicks present at the nest site. I then continuously recorded their presence and activity such that I was able to determine (1) the percentage of time that parents were absent from the

nesting territory during the low-tide foraging period and (2) the proportion of time parents foraged on the nesting territory during the low-tide foraging period. Parents were considered absent from the territory if they were observed departing the territory they defended as a breeding site or if they could not be located on the nesting territory during the observation period.

Statistical Analysis

Use of Nesting Territories for Foraging (2006)

I used a mixed model with repeated measures to examine the percentage of time breeding adults were present at their territory during the low-tide foraging period in relation to a suite of independent variables. Nest identification was included as a random term in the model and also was used as the subject of the repeated measures statement. The proportion of total time attended in relation to total time available was the dependent variable. I combined the amount of time each parent was present at the nesting territory during the one-hour observation period to derive a measure of total attendance. For example, if parent 1 was on the territory for 50 min of a 60 min observation period, and parent 2 was on the territory for 40 min of the same 60 min observation period, then the percent time attended = $((50 + 40)/120)) = 0.75$. Fixed factors included nest fate (fledged ≥ 1 chick or failed), brood size $(1 - 3)$, nesting attempt number $(1 - 3)$, chick age (d), and chick age^2. Two way interaction terms included in the model were chick age * brood size, and chick age^2 * brood size. The variable, chick age^2 was included to allow for a nonlinear relationship between chick age and the dependent variable. I used a manual

backward-selection process and deleted terms with $P > 0.10$ at each step. Percentages were transformed using the arc sine root transformation to standardize the variance.

To assess possible compensation within pairs (i.e., if parent 1 was on the territory longer than parent 2, or vice versa), I used a mixed model with repeated measures and analyzed the difference in attendance times between parents (i.e., parent 1 attendance time – parent 2 attendance time). Nest identification was included as a random term in the model and also was used as the subject of the repeated measures statement. The same factors, random variables, and procedures described above were used in this analysis as well.

Behavioral Traits of Foraging Oystercatchers (2007)

The second year of this study was conducted during the breeding season of 2007 and aimed to compare diet and behavioral traits of oystercatchers foraging in two different oyster bays. Observations were conducted in Sewee Bay (no nesting activity) and in the southwestern section of Bulls Bay (active nests throughout the bay) within the Cape Romain Region (32º 49'-33º 05' N, 79º 20'-79º 45' W; Fig. 3.1). Sewee Bay is a shallow bay (0.3 m - 1.5 m) approximately 2 km^2 in area and located 10 km south of Awendaw, South Carolina. Sewee Bay is a naturally formed water body comprised of tidal creeks and shellfish reefs bordered by the Atlantic Intracoastal Waterway to the West and protected from the open Atlantic Ocean by Bull Island to the East. Bulls Bay is a shallow bay (0.15 m - 2.7 m) located within the Cape Romain National Wildlife Refuge. Shellfish reefs are located within the intertidal zone along the perimeter of Bulls Bay. Shellfish reefs in the Cape Romain Region contain primarily eastern oysters

(*Crassostrea virginica*) and ribbed mussels (*Geukensia demissa*). Shellfish reefs are exposed by the tide twice each day, and depending on wind speed, wind direction and moon phase, shellfish reefs can be exposed from two to 10 hours.

Foraging data were collected in Sewee Bay and southwest Bulls Bay from May to July 2007. Data also were collected in these locations during winter 2006 and methods followed those developed for that study (C. Hand, unpubl. data). Within each bay two sectors that could be accessed during low tide were chosen within which foraging observations were conducted. The Sewee Bay sectors were each accessible from the Sewee Bay channel while the Bulls Bay sectors were each accessible from Venning Creek and Anderson Creek. Within each sector, two or three observation points were marked. Observation points in both bays were spaced 275 to 400 m apart. Logistical constraints prohibited uniform spacing of observation points. In Sewee Bay, the observation points (n = 6) were located on oyster reefs and were spaced along the main channel which provided reliable boat access to a variety of reefs even at low tide. In Bulls Bay, observation points (n = 4) were located on shell mounds or marsh along the shoreline (Fig. 3.1).

Observations were conducted either during falling or rising tides. I defined a falling low tide as the time from which oyster reefs were first exposed (i.e., when the tops of oyster shells were just visible at water's surface) until book low tide (Tidelog Southeastern edition, Pacific Publishers, 2007) and a rising low tide period as beginning at book low tide and continuing until all oyster reefs in the scan area were fully submerged. Observations periods generally lasted 2.5 to 4.5 hours.

Focal animal observations were used to collect diet and foraging behavior data from individual oystercatchers at each observation point. I randomly determined the order in which sectors were visited among dates and randomly determined the order in which points were visited within each sector within a low tide period. Due to logistical constraints (i.e., difficulty of moving from one sector to another during low tide) data were not collected from multiple sectors within a low tide period although data were collected from multiple observation points within a sector within a low tide period. I was able to move among observation points within a sector. Once at a point I chose a random compass bearing and searched for an oystercatcher at that bearing within *ca.* 120 m of the observation point. This distance was chosen as a limit because preliminary observations indicated that it was difficult to identify prey items of foraging oystercatchers > 120 m from the observation point. If no individual was present at the randomly assigned bearing I proceeded clockwise until an individual was located. Once a foraging oystercatcher was located, a focal animal observation was initiated. A focal observation ceased when the individual flew off, walked out of view, or ceased foraging for $\geq$ one minute. During the focal observation I identified the prey item consumed by that individual for a single feeding event, where a feeding event was defined as the location and consumption of a single prey item by an oystercatcher. Focal observations ranged from 1 to 11 feeding events per bird. During each low tide period I moved between observation points within each sector. I departed an observation point after completing two scans (360 degree rotations) and observing every bird in each of those scans or after observations were conducted from one point for one hour, whichever occurred first. If no foraging

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oystercatchers were observed during the first 360º scan, I waited ten minutes before initiating the second scan.

During focal animal observations the prey type was identified to the lowest taxonomic class possible and the size of each piece consumed was estimated. When estimating the size of a prey item, portions of the organism that were not ingested, such as the shell and flesh that was left in the shell, were not included. Items that could not be identified (e.g., obstructed view) were omitted from analyses. I defined prey size classes based on the dimensions of the oystercatcher's bill following Tuckwell and Nol (1997). {Direct comparisons of volumes of prey found by Tuckwell and Nol (1997) were not made because class sizes used to estimate volume differed}Class 1 (<0.99 ml, midpoint 0.5 ml) consisted of pieces less than ¼ of the length of the oystercatcher's bill, class 2 (1.0 - 5.0 ml, midpoint 3.5 ml) pieces were between ¼ and 1 bill length, and class 3 (> 6.0 ml, midpoint 6 ml) pieces were as long as the bill and were difficult to swallow. I also observed pieces of prey items that were too small to be readily visible while they were being handled and therefore added an additional class size of class 0 (< 0.5 ml, midpoint 0.25 ml). The total volume of each prey item consumed was estimated by summing the midpoint volume estimates of the size class for all of the individual pieces (Tuckwell & Nol 1997).

In addition to identifying prey items during focal observations I also recorded search times and handling times for successful feeding events for each focal oystercatcher. Search time was defined as the duration of time (sec) between the consumption of one prey item and the beginning of handling for the next item. Handling time included capture and consumption and so was defined as the duration of time from

the initial stab until the oystercatcher consumed the item and subsequently began

searching for the next item (Cadman 1980, Tuckwell and Nol 1997). If an oystercatcher

briefly stopped searching or handling to preen, to be vigilant, or to engage in other non-

foraging behavior, the time spent engaged in other activities was not included in the

search and handling times (C. Hand). If an oystercatcher stopped foraging for at least one

minute, observations of that bird were discontinued.

In order to assess relative abundance of oystercatchers during each observation

period I conducted 360º scans from observation points and counted the number of birds

visible within 120 m of the observation point. These were conducted ≥ 2 times for each

observation point in conjunction with focal animal observations. I classified each

oystercatcher observed during these counts as either actively foraging or as not foraging.

Statistical Analysis (2007)

Behavioral Traits of Foraging Oystercatchers (2007)

Statistical analysis aimed to determine if there were differences in searching

times, handling times, proportion of prey types consumed, and volume of prey consumed

of foraging oystercatchers between Bulls Bay and Sewee Bay. I also tested for

differences in handling times and prey volumes among prey types across both study sites.

Difference in proportion of prey types consumed between locations was assessed with

Pearson's Chi square test. For all other analyses, I used a generalized linear mixed model

with location, prey type and location * prey type as independent variables. Each

individual bird within each location was considered a random term in the model. Prior to

analysis, searching times and handling times were averaged according to prey type for

each bird observed to avoid pseudoreplication (Tuckwell & Nol 1997). I used the scan data to determine if there were differences in total number of birds, or number of birds foraging between locations. I also tested for differences in total number birds, or number of birds foraging based on tidal stage. The daily maximum number of birds were averaged for each location prior to analysis.

<div align="center">Results</div>

Use of Nesting Territories for Foraging (2006)

I conducted 39, one-hour long observations of breeding pairs in 2006: 17 observations of 7 nests in Bulls Bay, and 22 observations of 6 nests along the AICW. There was no significant difference ($\chi^2 = 4.04$, $P = 0.13$) in mean brood size between Bulls Bay (1.7 ± 0.6 chicks) and the AICW (1.6 ± 0.8 chicks). The mean chick age in Bulls Bay (28.4 ± 2.6 d), however, was significantly greater ($t_{37} = 3.8$, $P = 0.0005$) compared to the mean chick age along the waterway (16.4 ± 1.9 d). The number of nesting attempts in Bulls Bay (1.2 ± 0.1) also was significantly less ($\chi^2 = 11.3$, $P = 0.003$) compared to the waterway (2.1 ± 0.2). Therefore attendance data from each location were analyzed separately.

Combined adult attendance at the nest site ranged from 50% to 98% on the waterway and 38% to 100% in Bulls Bay (Table 3.1). On the AICW, adult attendance at the nest site was most strongly related to eventual fledging success (F = 6.58, $P = 0.02$). Attendance was lower at waterway nests (i.e., more time was spent foraging away from the nest mound) that successfully fledged a chick compared to nests that failed to fledge any chicks (Fig. 3.2). For pairs nesting in Bulls Bay, fledging success (F = 5.09, $P = 0.065$) and chick age * brood size (F = 3.97, $P = 0.08$) best predicted adult attendance. In

<div align="center">50</div>

contrast to the AICW, attendance by parents tended to be higher at nests that successfully fledged a chick in Bulls Bay (Fig. 3.2). There was a weak negative relationship between percent attendance and the interaction term chick age * brood size. Attendance decreased with chick age and did so most strongly in broods with three chicks ($t_1 = 4.6$, $P = 0.13$) in Bulls Bay.

There was no significant difference in attendance between adults within pairs in either location ($P = 0.17$ for both). In Bulls Bay parents were present for the entire observation period during 29% of observations and on the AICW parents were present for the entire observation period during 9% of observations.

Behavioral Traits of Foraging Oystercatchers (2007)

I conducted foraging observations during 12 days in Sewee Bay and 12 days in Bulls Bay between May and July, 2007. The total number of birds observed during one low tide scan ranged from 0 – 7 and the total number of birds foraging ranged from 0 – 3. The mean maximum number of birds observed per day differed slightly by location ($F_{1,9} = 3.66$, $P = 0.08$) as did the mean maximum number of birds engaged in foraging ($F_{1,9} = 4.83$, $P = 0.05$) per day. In each case there were more individuals in Bulls Bay compared to Sewee Bay (Table 3.2). There were no differences in the mean maximum number of birds observed per day or mean maximum number of birds engaged in foraging per day between tidal stages ($F_{1,9} > 1.2$, $P > 0.20$ for each).

Oystercatchers foraged predominantly on eastern oysters (*Crassostrea virginica*) (Fig 3.3). I also observed oystercatchers foraging on ribbed mussels (*Geukensia demissa*), items that were too small to identify by sight (size class 0), and unknown items that although large enough to be observed could not be identified (Fig 3.3). There were no

significant differences in the proportion of each prey item consumed (Fig. 3.3) ($X^2 = 6.0$, df = 3, $P = 0.11$). The volumes of prey consumed differed ($F_{3, 69} = 22.19$, $P = < 0.0001$) among individual prey items. Mussels were the largest prey item consumed (2.7 ml ± 0.36) followed by oysters (1.6 ml ± 0.14), unknown (0.43 ml ± 0.37) and size class 0 items (0.33 ml ±0.16). Handling times also differed with the interaction of prey type and location ($F_{3, 66} = 3.43$ $P = 0.02$). Handling time for mussels in Bulls Bay (55.0 s ± 3.2) was the longest of any prey type ($t_{66} = 2.93$ $P = < 0.005$ for all) (Figure 3.4). Size class 0 items had the shortest handling times in both locations (Sewee Bay 16.0 s ± 4.2, Bulls Bay 13.9 s ± 2.2) and these times were significantly shorter than handling times for oysters in Sewee Bay (25.1 s ± 3.7) and mussels in Bulls Bay. Searching time ($F_{1, 82} = 0.45$, $P = 0.51$) and total volume of each prey item consumed ($F_{1, 85} = 1.13$, $P = 0.29$) did not differ between Sewee Bay and Bulls Bay (Table 3.3)

<div align="center">Discussion</div>

Use of Nesting Territories for Foraging (2006)

Rates of parental attendance at the nest territory during the foraging period tended to be higher for oystercatchers nesting in Bulls Bay compared to those nesting along the waterway. Furthermore, fledging success was higher in Bulls Bay compared to the waterway in 2006 not only for the pairs of birds observed in this study but also from a larger sample of pairs that were monitored as part of a broader study of oystercatcher reproductive success (see Chapter 2). Higher reproductive success in Bulls Bay in 2006 was likely due at least in part to lower rates of nest overwash and predation (see Chapter 2). However, the higher rates of attendance on the nesting territories during foraging periods in Bulls Bay also may have contributed to higher reproductive success there. Two

components of the study areas that may have affected reproductive success and also may have been related to the differences observed in attendance between the two study areas are the proximity of the nest territory to the foraging area and the physical configuration of the nest territory as it relates to foraging.

Studies examining the reproductive success of European Oystercatchers (*Haematopus ostralegus*) found that pairs with contiguous nesting and feeding areas (i.e., resident birds) had higher fledging success compared to those pairs that commuted to feeding territories (i.e., leapfrog birds; Ens et al. 1992). This difference was attributed primarily to decreases in meal delivery rates in leapfrog territories brought about by the need for parents to commute to obtain food and the inability of chicks to accompany parents directly to feeding areas. During my study, American Oystercatchers nesting in Bulls Bay occupied territories that appeared to function like resident territories. Here, both parents typically foraged at the edge of the nest site and chicks often accompanied parents resulting in frequent feedings. In contrast, pairs along the AICW occupied territories that were more similar to the leapfrog territories described by Ens et al. (1992). In this Region the waterway consisted of a deep channel with interspersed narrow strips of shell mounds on either side. During low tide, oysters were exposed in tidal creeks adjacent to the waterway but not always along the nesting shell mounds. This created a discontinuous mosaic of shell islands along the channel of the waterway with few nest sites adjacent to oyster reefs. Along the waterway one member of a nesting pair often left the territory to forage while the other parent remained. Chicks along the waterway also were unable to accompany parents to the feeding area.

Physical characteristics of nesting and feeding territories such as slope and structure also may influence provisioning behavior thus affecting chick survival. In a study of reproductive success and foraging territory structure in Black Oystercatchers (*Haematopus bachmani*), hatching success was higher and more chicks fledged from breeding territories of intertidal sites with shallow slopes compared to those with steeper slopes (Hazlitt 2001). Pairs nesting on territories with shallow slopes provisioned chicks at higher rates than those on steeper slopes. Hazlitt (2002) suggested that the higher rates of provisioning there were a function of chicks from shallower territories accompanying parents to the intertidal area during foraging bouts resulting in more frequent feeding (Hazlitt et al. 2002). Although I did not measure slope steepness in this study it appeared that intertidal areas adjacent to nest mounds along the waterway were steeper compared to those in Bulls Bay where nesting territories were characterized by shallow sloping shell mounds that opened to intertidal oyster reefs along the shoreline. Steeper slopes along the waterway would be consistent with the higher wave energy generated by heavy boat traffic there. I also observed boat wakes on the waterway reaching halfway up and sometimes completely over nest mounds. These characteristics, along with the lack of abundant oyster reefs directly adjacent to the waterway, likely hinder chicks from foraging on the nesting territory and may have contributed to reduced reproductive success there.

Landscape of the foraging habitat as it relates to visibility may also influence vigilance of parents and parental defense of chicks resulting in higher fledging success. For example, in Virginia Nol (1989) found that parent American Oystercatchers that fed on large and nearby territories that also had high visibility raised more chicks than those

with small or no nearby foraging territories where visibility was poor. In the Cape Romain Region both parents often remained on the nesting territory to forage in Bulls Bay and hence were likely able to maintain relatively high levels of vigilance. In contrast, oystercatchers that nested along the waterway and commuted to forage were not likely to maintain as high a level of vigilance as resident parents in Bulls Bay. This may be one reason why predation rates on eggs were higher along the waterway compared to Bulls Bay (see Chapter 2).

Lower hatching success and higher rates of loss of young chicks along the waterway in 2006 compared to Bulls Bay also resulted in older chicks being more prevalent in Bulls Bay during this study (See Chapter Two). I found that attendance decreased with chick age and was lowest in the single three-chick brood I observed in Bulls Bay. Lower attendance for pairs with older chicks may occur because energy needs of chicks increase as they age (Drent & Klaassen 1989) and hence parents may need to procure additional resources. Increased provisioning rates with brood size and brood age have also been observed in Black Oystercatchers (Hazlitt 2002).

Behavioral Traits of Foraging Oystercatchers (2007)

South Carolina supports *ca*. 1/3 of the eastern race of American Oystercatchers during the nonbreeding season, with the majority in the Cape Romain Region (Sanders et al. 2004) including many migratory and juvenile birds. During wintering foraging observations the maximum number of birds observed during a single scan in Sewee Bay and in Bulls Bay were 41 and 24, respectively (C. Hand unpublished data). During the breeding season, however, numbers of oystercatchers in either Sewee Bay or Bulls Bay

were much smaller during foraging observations. The larger numbers of birds observed in Bulls Bay compared to Sewee Bay during the breeding season was most likely because oystercatchers were also nesting along the perimeter of Bulls Bay and often foraged adjacent to their nesting territories. Unlike Bulls Bay, there is no nesting habitat within Sewee Bay hence breeding season flocks may be smaller there.

Few data are available on the diet of oystercatchers (Humphrey & Nol 1994). The primary item in the diet of oystercatchers in both study areas within the Cape Romain Region in 2007 was eastern oysters. Tuckwell & Nol (1997) examined the foraging behavior of oystercatchers during the winter at a commercially harvested oyster reef in Virginia and also found that oysters were the dominant prey type. The second most common prey type in my study was size class 0 items. While size class 0 items were too small to identify to species, it is likely that they were small oysters based on the manner in which they were handled by oystercatchers.

Oystercatchers in the Cape Romain Region also foraged on ribbed mussels during the breeding season, although handling times were longer for mussels compared to other prey items. Ribbed mussels composed a small percentage of prey consumed by wintering oystercatchers in Virginia (Tuckwell & Nol 199), and may be a more prevalent forage item during the summer elsewhere especially for birds provisioning chicks. While observing foraging parents in 2006, adults were observed feeding chicks ribbed mussels and opened mussel shells were often found at nesting territories of oystercatchers with chicks. Nol (1989) also found that oystercatcher parents breeding in the Chincoteague area of Virginia fed their chicks almost exclusively on ribbed mussels. Mussels may therefore compose a greater percentage of diet of oystercatchers in the Cape Romain

Region during the summer than at other times (C. Hand unpublished data). The availability of ribbed mussels during the tidal cycle also might influence the prey choice of oystercatchers despite the longer handling times than other prey types. Unlike oysters that must remain closed at low tide to avoid desiccation, ribbed mussels are able to respire in dry conditions and can remain gaping at low tide (Lent 1968) providing oystercatchers an opportunity to pry them open and feed on them for longer periods of the tide cycle. Oystercatchers are able to remove entire ribbed mussels from oyster reefs in contrast to oysters that must be pried open and meat removed while at the oyster reefs. Parent birds were observed returning to the nest site with intact ribbed mussels and opening the shell in front of chicks for chicks to feed on the inside contents.

Eastern oysters were the major forage items for oystercatchers in the Cape Romain Region during the summer months. Oyster harvesting occurs both commercially and recreationally in South Carolina and removal of shell from mounds is permitted by the state for commercial clam and oyster mariculture (Sanders et al. 2008). Along with habitat loss, commercial fisheries may pose a threat to shellfish eating birds. Researchers in Europe investigated the effectiveness of marine protected areas on the condition and survival of the European Oystercatcher (*Haematopus ostralegus*) and found that individuals foraging in unprotected areas had less shellfish in their diet and poorer body condition, the latter of which was correlated with higher probability for mortality (Verhulst et al., 2004). As demand for commercially produced shellfish increases, foraging areas of shellfish eating birds will be influenced. Pressure from coastal development as well as threats of disease, over-harvesting or alteration of water flow and salinity may negatively alter the quality or composition of oyster reefs in the Cape

Romain Region and ultimately the food resources for this species. Altered foraging areas may have an especially negative effect for breeding oystercatchers on the waterway that commute to foraging locations from their nesting sites and already appear to experience lowered reproductive success. Understanding the value of foraging resources, particularly how they relate to reproductive success, is important for protecting and, if necessary, restoring resources in the future. There is also need for future study to determine quality of prey items included in oystercatcher diet such as energy density and lipid content which may reveal other aspects of foraging ecology and factors which may contribute to positive reproductive success. Management should focus on quality foraging areas as well as areas of positive reproductive growth.

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Table 3.1 Percentage of time (one hour observations) parent American Oystercatchers were present within the nesting territory during low-tide foraging periods, Cape Romain Region, South Carolina, May - July 2006. Percentages are reported as raw values. n = number of observation periods.

Location	Range (%)	Mean (%) ± SE	Median (%)	Mode (%)
Waterway (n=22)	50-98	81.0 ± 2.7	82	81
Bulls Bay (n=17)	38-100	88.0 ± 2.7	91	100

Table 3.2 Number of American Oystercatchers observed during foraging scans in the Cape Romain Region, South Carolina May-July 2007.

	Total				Foraging			
	Max	Min	Max average (SE)	*P*	Max	Min	Max average (SE)	*P*
Sewee Bay	5	0	1.75 (0.64)	0.055	2	0	0.69 (0.34)	0.088
Bulls Bay	7	0	3.47 (0.64)		3	0	1.34 (0.34)	

Table 3.3 Comparison of mean search times (SE), mean handling times (SE) and mean estimated total volume (SE) of prey types consumed by American Oystercatchers between two locations in the Cape Romain Region, South Carolina May-July 2007. *N* **is number of individuals.**

| Comparison	Sewee Bay	N	Bulls Bay	N	t	*P*
Search times (s)	19.9 (7.7)	19	25.4 (3.2)	67	0.67	0.51
Handling times (s)	22.0 (4.0)	19	27.4 (1.6)	68	1.26	0.21
Total volume (ml)	1.4 (0.28)	19	1.1 (0.11)	68	-1.06	0.29
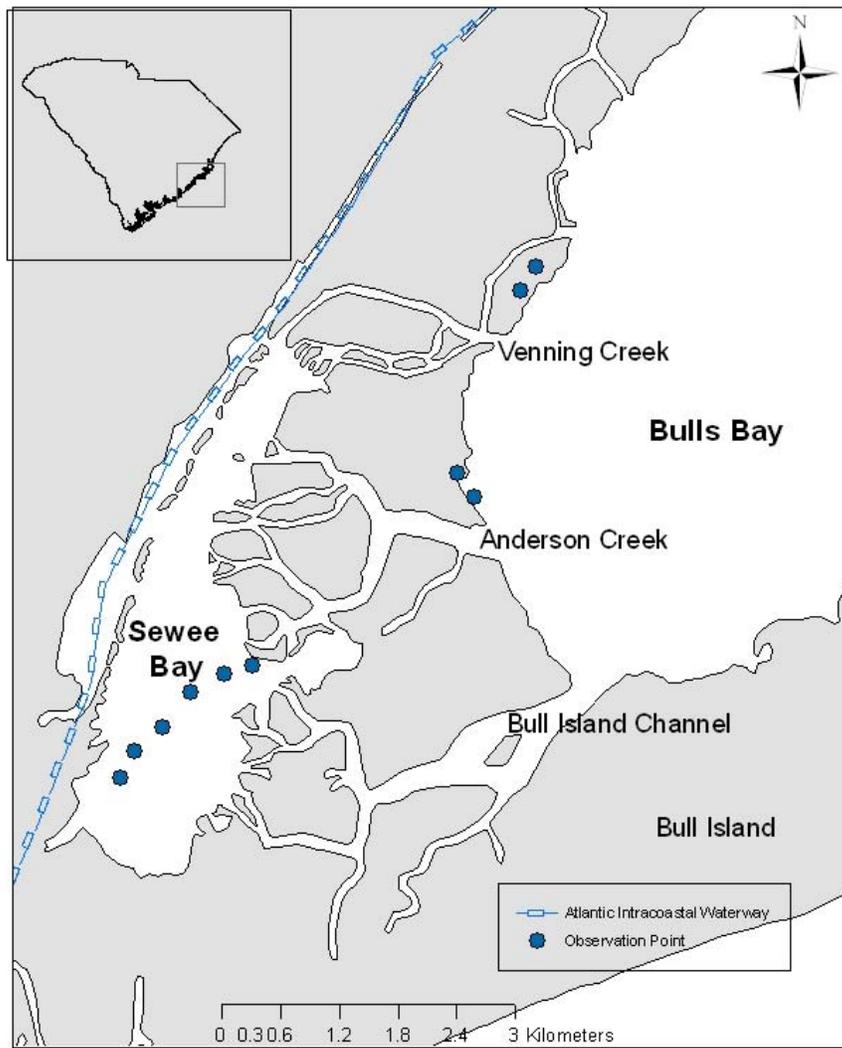
Figure 3.1 Study area within the Cape Romain Region, South Carolina 2007 showing locations of observation points.
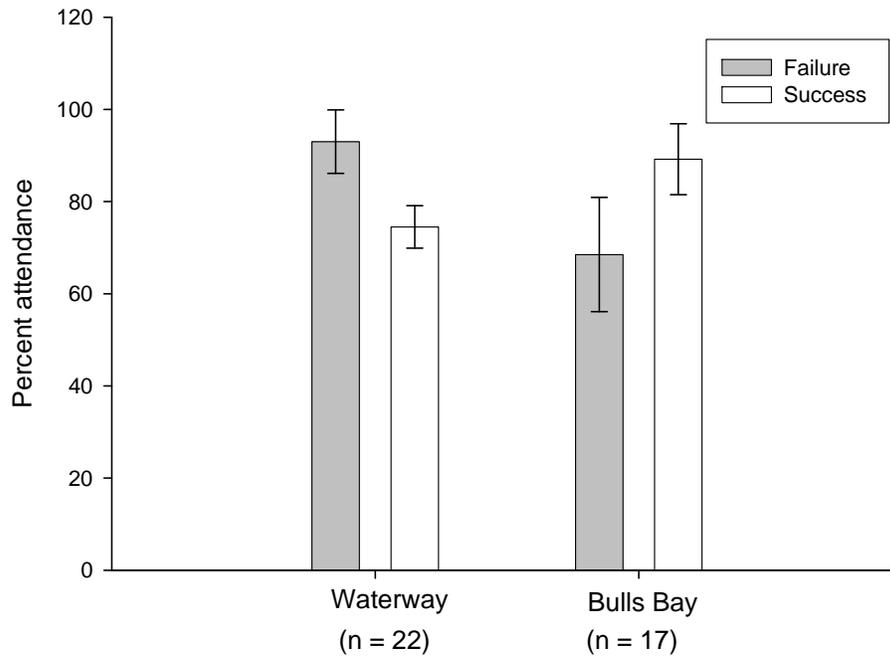
Figure 3.2 Percent of nest attendance (±1 SE) and nest fate of American Oystercatcher pairs during the foraging period in the Cape Romain Region, South Carolina, May – July 2006. Parentheses indicate number of observation periods.
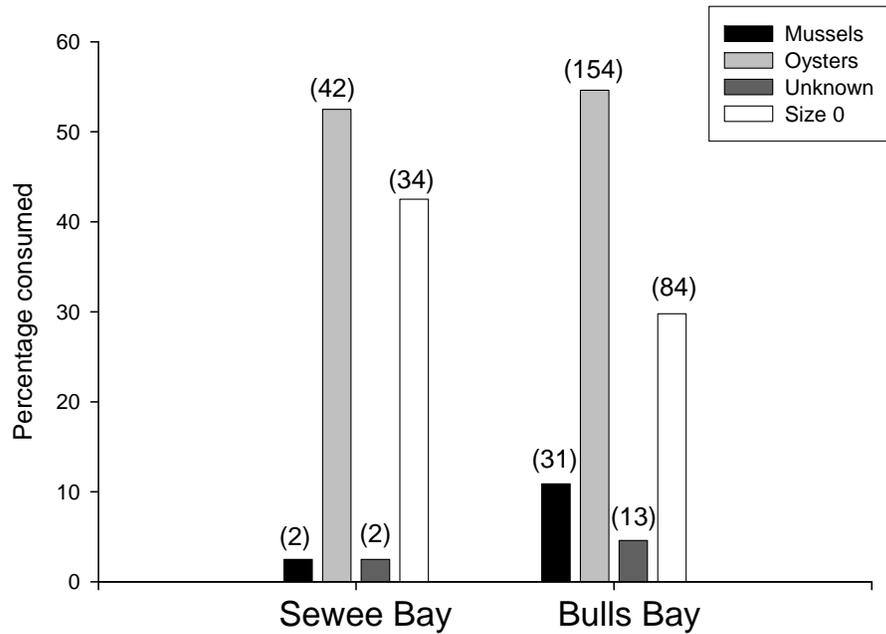
Figure 3.3 Prey types and proportions consumed by American Oystercatchers in two locations within the Cape Romain Region, South Carolina, May – July 2007. Parentheses indicate sample sizes. Size 0 were items too small to be readily visible while they were being handled but are expected to be oysters.
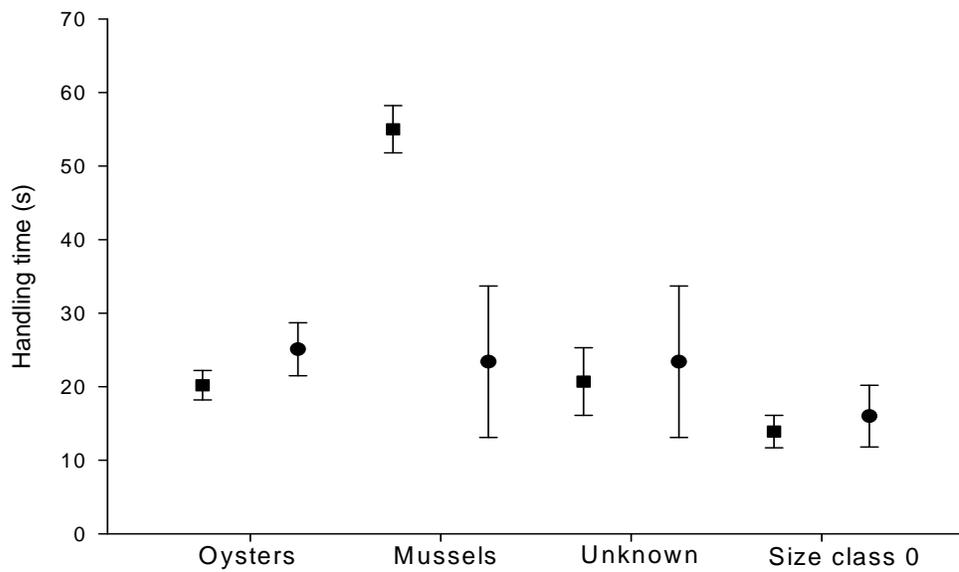
Figure 3.4 Handling times for prey items consumed in two locations within the Cape Romain Region, South Carolina, May – July 2007. Squares indicate Bulls Bay, circles indicate Sewee Bay. Size 0 were items too small to be readily visible while they were being handled.

CHAPTER FOUR

CONCLUSION

American Oystercatchers are long lived shorebirds with variable annual rates of reproductive success. Coastal development and disturbance due to humans as well as predation of nests and overwash of nest sites are threats to this species during the breeding season. I measured reproductive success and determined reasons of nest failure in an area of high nesting density of oystercatchers in South Carolina. I also investigated foraging attributes of parent oystercatchers and prey choice and efficiency of oystercatchers during the breeding season in several primary foraging areas along the coast.

The second chapter of this thesis "Reproductive Success of American Oystercatchers in the Cape Romain Region, South Carolina," compared reproductive success including hatching success, fledging success and productivity of oystercatchers nesting on shell mounds in two different nesting areas within the Cape Romain Region: the Atlantic Intracoastal Waterway and Bulls Bay. Reproductive success varied between locations and between years with the highest success achieved in Bulls Bay. Flooding of nests due to overwash was the primary identified cause of nest failure followed by avian predation. Oystercatchers in both locations frequently re-nested after nest failure.

Chapter three, "Foraging Behavior of American Oystercatchers During the Breeding Season in the Cape Romain Region, South Carolina", examined the proportion of time that parent oystercatchers were absent from the nesting territory during the low

tide foraging period in relation to fledging success in two different nesting areas of the Cape Romain Region: the Atlantic Intracoastal Waterway and Bulls Bay. Oystercatchers nesting along the waterway spent more time away from the territory and fledged fewer chicks than parent oystercatchers nesting in Bulls Bay. I also determined foraging efficiency of oystercatchers foraging in two oyster reefs within the Cape Romain Region: Sewee Bay and Bulls Bay. Oystercatchers were more abundant in Bulls Bay than in Sewee Bay and oystercatchers foraged on primarily oysters in both bays during the breeding season.

Oystercatchers nesting in South Carolina appear to experience variable nest success in part due to rates of overwash of eggs. The number of re-nests and stable clutch sizes of sequential nest attempts suggests that the Cape Romain Region provides adequate resources for oystercatchers to invest into reproduction.