American Oystercatcher winter roosting and foraging ecology at Cape Romain, South Carolina

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American Oystercatcher *Haematopus palliatus* foraging areas, roost sites (diurnal and nocturnal) and prey items were identified. Eight adult oystercatchers were radioed during Dec 2003 to Feb 2004 in Cape Romain Region, one of the most important wintering sites for this species. Mean distance between capture site and two other diurnal high tide roosts was 1,819 m. Distances from mean center of foraging locations to nocturnal roosts were farther than to diurnal roosts. Nocturnal roost sites may contain more birds and be situated farther away from prime feeding areas in order to avoid predation by owls. Oystercatchers spent 53% of the time roosting and only 28% foraging when their feeding areas were exposed at low tide. Prey items were 94% oysters, 4% mussels and 3% unknown prey items. The combination of roost sites (diurnal and nocturnal) and abundant food may explain why the Cape Romain Region has historically and presently had a large concentration of oystercatchers.

INTRODUCTION

Many shorebirds throughout the Western Hemisphere are declining and research is needed to determine factors that limit populations (Brown *et al.* 2001). Avian studies often concentrate on breeding season ecology, but for most shorebirds winter is a substantial source of annual mortality (Evans & Pienkowski 1985, Goss-Custard 1982). Shorebirds are especially vulnerable because they concentrate at key sites during migration and winter, and spend most of the year on non-breeding sites (Evans 1991, Goss-Custard 1980). Habitat loss on wintering grounds can further reduce survival rates of shorebirds (Burton *et al.* 2006). Research is needed to explore prey availability and key landscape variables such as roost site availability and distance between roost sites and foraging areas (including nocturnal sites) to better understand why some non-breeding season locations are preferentially used (Brown *et al.* 2001, Rogers 2003). Identifying these factors is also important for understanding the effects of development and habitat alteration on shorebird survival, for conservation planning, and for designing shorebird refuges and mitigation efforts (Burton *et al.* 1996, Rehfisch 2003, Sanzenbacher & Haig 2002).

The American Oystercatcher *Haematopus palliatus* is one of many shorebird species thought to be declining and is considered a high priority species for conservation (Brown *et al.* 2001). Despite the fact that it is a large conspicuous shorebird, few studies have focused on American Oystercatcher ecology during the non-breeding season compared to during the breeding season (American Oystercatcher Working Group *et al.* 2012; yet see Cadman 1980, Hand 2008, Peters 2005 and Tuckwell & Nol 1997). The American Oystercatcher is a long-lived species with low reproductive rates (American Oystercatcher Working Group, *et al.* 2012); thus high annual survival is important for population stability and growth. Understanding the winter ecology of this species is a first step in developing management practices that can increase winter survival rates. This study expands knowledge of the American Oystercatcher's non-breeding season ecology by identifying areas used at low tide, roost sites (diurnal and nocturnal) and prey items in one of the most important North American wintering sites for the species.

STUDY AREA

The study was conducted in the Cape Romain Region, defined as the coastal area of South Carolina from Cape Romain National Wildlife Refuge south to Isle of Palms (32°49'–33°05' N, 79°20'–79°45' W, Fig. 1). Cape Romain National Wildlife Refuge is a site of International Importance for shorebirds (Western Hemispheric Shorebird Reserve Network 2012). The region consists of barrier islands, estuarine islands, salt water marshes, creeks and shallow bays. Intertidal oyster reefs, primarily consisting of Eastern oysters *Crassostrea virginica*, ribbed mussels *Geukensia demissa* and hard clams *Mercenaria mercenaria* occur along edges of creeks and in bays on mud flats.

Bulls Bay, near the northern boundary of the study area, is a 13-km long shallow bay bordered by barrier islands and typified by exposed mud flats at low tide. Marsh Island is a 19-ha island in Bulls Bay characterized by salt marsh and shrubby vegetation, with a narrow sandy beach and extensive oyster reefs. Marsh Island supports a large nesting colony of thousands of seabirds and wading birds and 20 pairs of American Oystercatchers (Ferguson *et al.* 2005). Bird Shoal, in Bulls Bay, is a sandy bar that is covered at high tide and is south of Marsh Island (Fig. 1).

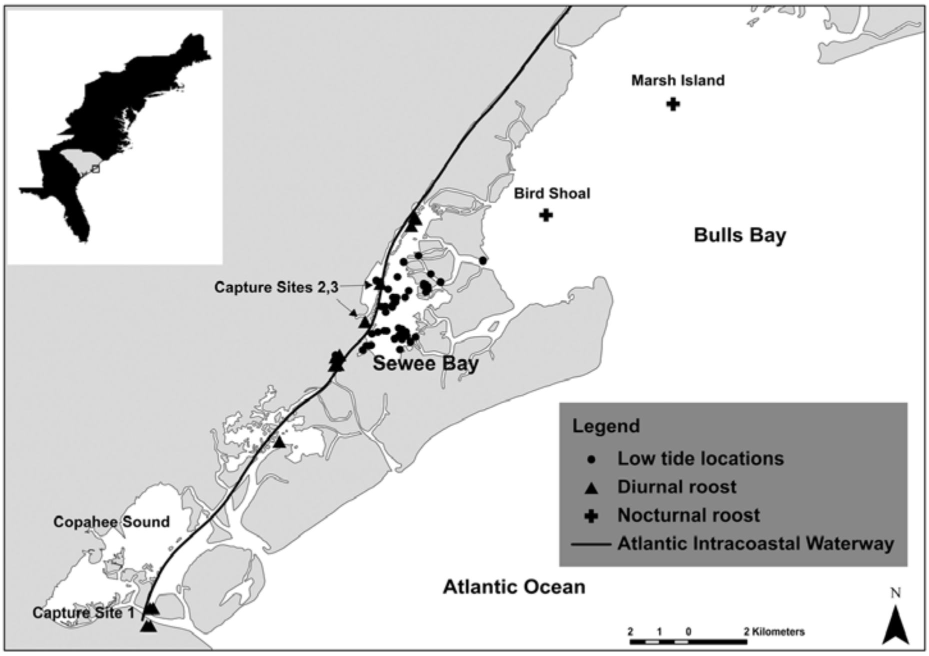

Fig. 1. Locations of American Oystercatchers captured at three diurnal high tide roosts and radio-tracked in Cape Romain Region, South Carolina, during winter 2003–2004. Oystercatchers were located during nocturnal searches at Marsh Island and Bird Shoal. Oystercatchers captured at Sites 2 and 3 were also located during low tide in Sewee Bay.

The Cape Romain Region of South Carolina supports about one-fifth (1,900) of the wintering American Oystercatcher population on the Atlantic and Gulf coasts of the United States (Brown *et al.* 2005, Sanders *et al.* 2004). Migratory oystercatchers arrive in South Carolina in late August and leave as late as the beginning of April. The number of oystercatchers in the study area appears to be stable and peaks during December–February (Sanders *et al.* 2004). Oystercatchers from every Atlantic Coast state north of South Carolina with breeding season banding programs have been observed in Cape Romain Region during the winter, indicating that the Region is critically important for the entire U.S. Atlantic coast breeding population. Additionally, the oystercatchers that breed in the Cape Romain Region apparently remain year round (Sanders *et al.* 2004).

Tidal range during the study was –0.3 m to 2.1 m, (National Oceanic and Atmospheric Administration, Charleston Harbor predictions). During spring high tides, oystercatchers generally roost in flocks of 100–500, along with flocks of other shorebird species, on shell mounds adjacent to the Atlantic Intracoastal Waterway (AIWW), a linear waterway that runs northeast to southwest through the study area (Dodd & Spinks 2001). These shell mounds consist primarily of washed oyster shells. Food is scarce on these mounds thus shorebirds are rarely seen foraging on them. During tides below 1.6 m, oystercatchers and other shorebirds leave these high tide roosts and go to intertidal oyster reefs and mudflats (Hand *et al.* 2010, Tuckwell & Nol 1997, pers. obs.).

METHODS

On three days in Nov and Dec 2003, cannon nets were used to capture American Oystercatchers at high tide at three locations on the AIWW (Fig. 1). Eight adult oystercatchers, aged by bill and eye color, were fitted with unique frequency 5 g radio-transmitters with an estimated battery life of three months. Feathers were first clipped with scissors from a small area on the oystercatchers' backs between the scapulars. A piece of cheesecloth the same size as the radio was placed between the radio and the skin of the bird. Loctite® glue (Henkel Corporation) was used to fix the radio and cheesecloth to the back of the bird. One U.S. Geological Survey metal leg band and one unique engraved color band was also fitted to each oystercatcher.

Oystercatchers were tracked from Dec 2003 to Feb 2004. One oystercatcher per day was followed for approximately four hours when water levels were <1.0 m. Tracking occurred at different times of day and tidal stage (rising and falling tides) based on weather and staff availability. Data collection did not begin until a focal oystercatcher was observed, which often took up to an hour after a signal had been located. Oystercatchers were tracked in a 5-m long boat using a hand held Yagi, 4-element antenna. Following oystercatchers at low tide was very difficult because of exposed mud and oyster reefs and visually observing the bird was not always possible after a tracking session started.

When possible, the focal bird was observed continuously with binoculars or a telescope placed on the front deck of the boat. Every 15 minutes the focal oystercatcher's behavior at that moment was recorded. Behavior was recorded as either: roosting (sleeping, preening, bathing, or standing), flying, foraging, aggressive activity, or unknown (if the bird was not in view). The number of oystercatchers within about 25 m of the focal bird was also recorded as a measure of conspecific density. For focal oystercatchers observed foraging, bout duration was also recorded. Forage bout duration was defined as the number of consecutive minutes a focal individual was observed foraging, starting at the time the bird was first observed to the time the bird stopped foraging or moved out of view. Oystercatchers often went out of view behind oyster reefs during observation periods, so recorded foraging times were typically less than actual foraging bouts. Prey items were categorized as oyster, mussel or unknown. The number and species of prey items taken during foraging bouts were recorded.

All locations were based on visual observations and recorded with a Global Positioning Unit after the focal oystercatcher left a site, or marked on aerial photos. Locations from aerial photos were plotted in ArcGIS (Esri 2009) and coordinates were obtained.

One day in January and one day in February, during a spring high tide, all radioed oystercatchers were located, so that three high tide roost locations (i.e. capture site, January roost, February roost) were identified for each individual. Because the AIWW is a linear waterway, the mean distance between the three high tide locations was calculated for each bird to examine high tide roost site fidelity. The AIWW was also searched visually at high tide at night with a spotlight to determine if shorebirds were roosting at diurnal roost sites, and locations of oystercatchers were identified on seven nights.

Several methods were used to describe oystercatcher use of foraging grounds. Minimum and maximum distance from foraging locations to capture site (a representative high tide roost location) was calculated in ArcGIS (ESRI 2009). The amount of habitat used during low tide by individuals was determined by calculating the 100% minimum convex polygon around all foraging locations using Hawth's Analysis Tools (Beyer 2004). The center of all foraging locations (i.e. mean center) was calculated for each oystercatcher using the mean center tool (Esri 2009). Means ±1 standard error are reported.

RESULTS

Diurnal tracking

Two of the radioed oystercatchers (birds 2 and 8) were captured at the southern extreme of the study area at Capture Site One and foraged in Copahee Sound, an area outside our focal area, so only six oystercatchers (i.e. those captured at sites Two and Three) were tracked during daylight hours (Fig. 1, Table 1). One of these six individuals (bird 7) lost its radio within one month of capture, thus it was only followed twice during diurnal low tide. Each oystercatcher was followed on an average of 4 (±1, range 2–7) days and for an average of 18 (±3, 8–28) hours. The aggregate time spent tracking was 107 hours over 25 tracking days. Tracking was carried out between 08:45 and 16:45, with 53% of tracking time taking place before noon and 47% after noon; 42% was during falling tide and 48% during rising tide. Mean minimum convex polygon of low tide locations for all oystercatchers was 178 ha. Mean distance between capture site and two other diurnal high tide roosts was 1,819 m (Table 2).

Nocturnal tracking

Each oystercatcher was located 4 (±1, 1–7) times at night. Nocturnal search times were either just before dawn 05h45–07h15 (n = 3 nights) or just after dusk 17h55–20h55 (n = 7

Table 1. American Oystercatchers captured at high tide roosts during the day and radioed in Cape Romain Region, South Carolina, winter 2003–2004. Oystercatchers were located during nocturnal searches at Marsh Island and Bird Shoal. Results are ± standard error.

Bird	Days tracked at low tide	Min convex polygon of foraging locations (ha)	Min distance from capture site to foraging location (m)	Max distance from capture site to foraging location (m)	Distance from capture site to Marsh Island (no. of times located) (m)	Distance from capture site to Bird Shoal (no. of times located at) (m)
1	4	82	796	2,952	5,803 (3)	7,227 (4)
2						6,164 (4)
3	3	235	2,261	3,614	12,974 (2)	7,227 (3)
4	4	122	467	1,976	11,808 (1)	6,164 (4)
5	5	152	873	2,257	11,808 (2)	6,164 (4)
6	7	295	337	2,476	12,974 (1)	
7	2	179	439	1,483		19,198 (1)
8						19,198 (4)
Mean	4 ±1	178 ±32	862 ±293	2,460 ±306	11,074 ±1343	8,918 ±2388

Table 2. American Oystercatchers captured at high tide roosts during the day and radioed in Cape Romain Region, South Carolina, winter 2003–2004. Oystercatchers were located during nocturnal searches at Marsh Island and Bird Shoal. Results are ± standard error.

Bird	Distance between three high tide diurnal roosts (m)	Distance from center of foraging locations to capture site (m)	Distance from center of foraging locations to Marsh Island (m)	Distance from center of foraging locations to Bird Shoal (m)
1	2,662 ±1169	1,610	11,372	5,619
2	1,691 ±708			
3	1,058 ±456	2,804	8,691	2,675
4	734 ±367	959	13,439	7,648
5	1,873 ±386	1,804	12,337	6,358
6	1,235 ±560	1,123	11,073	5,184
7	4,853 ±2371	1,196	12,465	6,699
8	447 ±162			
Mean	1,819 ±498	1,583 ±276	11,563 ±670	5,697 ±699

nights). Mean tide height during nocturnal tracking was 1.1 m (±0.1, 0.1–1.6). Radioed oystercatchers were found on Marsh Island when tides were 1.4–1.6 m and Bird Island Shoal when tides were 0.1–1.4 m. The geometric centers of Bird Shoal and Marsh Island were used for estimating distances in ArcGIS, because identifying exact locations of oystercatchers was not possible in the dark. Mean distance from diurnal capture site to Marsh Island was 11,074 m and to Bird Shoal 8,918 m (Table 1). Distances from mean center of foraging locations to nocturnal roosts were farther than to the capture site or diurnal roost (Table 2). No oystercatchers or other shorebirds were observed on the AIWW during nocturnal searches.

Behavioral observations

A total of 416 focal behavioral observations were recorded: 220 (53%) of roosting, 117 (28%) of foraging, 55 (13%) of unknown behavior, 16 (4%) of flying and 8 (2%) of aggressive behavior. Conspecific density during foraging observations was 2.9 (±0.2, 1–10, n = 108) oystercatchers with a radius of 25 m from the focal bird; during roosting 43.4 (±4.6, 1–295, n = 220) oystercatchers; and during aggressive behavior 4 (±1, 2–9, n = 8) oystercatchers. In addition, 708 minutes of more detailed foraging data were collected, revealing an average foraging time of 11 ±1 minutes per bout (1–51 minutes, n = 66). Prey items consisted of oysters 389 (94%; 1–48 per foraging bout), mussels 10 (4%; 1–2) and unknown items 14 (3%; 1–9). Oystercatchers ate 0.6 ±0.1 prey items/minute during observations.

DISCUSSION

Oysters were the primary food eaten by American Oystercatchers in this study. Similarly, Hand *et al.* (2010) found that during the winter in Cape Romain Region, 95% of the prey items consumed were oysters, 4% ribbed mussels and <1% were unidentifiable items. In Virginia, Tuckwell & Nol (1997) also found that oystercatchers ate primarily oysters in winter but mussels and oysters in autumn.

At low tide, on average oystercatchers occurred at lower densities when foraging (about 3 individuals within 25 m) than when roosting (about 43). Increased bird density during feeding can reduce rates of food intake because of interference by other birds (Goss Custard 1980), so that lower densities during foraging are expected. At low tide, even when oyster reefs were exposed and food was available, oystercatchers spent more time roosting than foraging. At low tide, when oystercatchers were not foraging they either walked to the top of the oyster reef where they roosted, or flew to an exposed oyster reef where other oystercatchers were roosting. Similarly Eurasian Oystercatchers *Haematopus ostralegus* may leave mussel beds to roost nearby during low tide (Moody *et al.* 1997). Larger densities were observed when roosting, perhaps because in groups birds are less vulnerable to predation (Pulliam 1973). Oystercatchers never flew to high tide roost sites at low tide. If available, low tide roosts sites near foraging areas are preferable to more distant high tide roost sites because they provide nearby feeding opportunities while reducing predation pressure (Rosa *et al.* 2006). Specific low tide roost sites on oyster reefs in the center of the bay (i.e. away from the edge of the marsh) were used consistently, presumably because visibility of any approaching predator was less limited. Oystercatchers spent 53% of the time roosting and only 28% foraging when their feeding areas were exposed at low tide. During scans of oystercatchers visible on exposed oyster reefs near fixed observation stations, Tuckwell & Nol (1997) and Hand *et al.* (2010) found that oystercatchers spent more time foraging than roosting. Because oystercatchers fly to low tide roost sites, observations at fixed sites may underestimate roosting time unless they include consistently used low tide roost sites (Zwarts *et al.* 1996). Because of the limited scope of this project we did not examine the proportion of birds foraging in relation to the time of low tide, although we suspect that the proportion foraging was greater at the beginning and ending of the low tide period. However, it is likely that the proportion foraging varies depending on the foraging behavior of individuals, weather, season and the duration that shellfish beds are exposed (Sitters 2000, Zwarts *et al.* 1996).

Hand *et al.* (2010) documented American Oystercatchers consuming prey at the same rate as this study (1 item/minute). Eurasian Oystercatchers are able to ingest food about three times the rate food can be digested. They can store considerable food in their esophagus, about 80 g of wet flesh, and this takes around five hours to digest (Kersten & Visser 1996). Because American Oystercatchers are also proficient at foraging (up to 48 oysters per foraging bout in this study), they are able and perhaps must spend considerable time roosting at low tide. Roosting at low tide as well as at high tide may be necessary to accommodate digestive pauses similar to those documented in Eurasian Oystercatchers.

During diurnal high tide searches, American Oystercatchers were only located in flocks along the AIWW and during low tide in Sewee Bay or Copahee Sound. A study of American Oystercatchers in Cape Romain Region with a larger sample size and covering a greater time span (tracking occurred from August to January) also found oystercatchers exhibited high site-fidelity to the area although local movement between roosts was common (Peters 2005, 2007). Peters (2005) found that the mean home range of adult oystercatchers at low tide was larger (685 ha) compared to this study (178 ha). Sample sizes of < 50 locations for individuals may negatively bias home range estimates (Otis & White 1999); thus this study reports minimum winter low-tide home ranges. Peters (2005) found that the mean distance from diurnal high tide roosts to the low tide locations of adult American Oystercatchers was 2064 m, similar to our figure of 1,819 m. In comparison, a 34-year study of five shorebird species found that the distance between high tide roosts and low tide areas used by Eurasian Oystercatchers (approximately 8 km) was lower than other study species (Rehfisch *et al.* 1996). Other studies of shorebirds during the winter show varying levels of site fidelity (Colwell *et al.* 2003, Pienkowski & Evans 1984, Warnock & Takekawa 2008). Western Sandpipers *Calidris mauri* in San Francisco Bay used roost sites in near proximity throughout the winter and the average distance between feeding and roosting sites was 2.2 km (Warnock & Takekawa 2008), although another study in California found Dunlin *Calidris alpina* can move up to 140 km in one season (Warnock *et al.* 1995). Typical prey items of oystercatchers are stationary and this may explain the lack of long distance movement observed in one season. For example oyster reefs provide predictable, abundant and accessible daily food.

The location of nocturnal shorebird roosts is often different from daytime roosts (Dickens 1993). Although diurnal high tide roosts spanned a 15.5 km length of the AIWW, all radioed oystercatchers were located at least once at either Bird Shoal or Marsh Island at night. At night, navigation to and near Marsh Island was very difficult due to reefs and shoals surrounding the island. Radioed oystercatchers not located during a particular night may have been on Marsh Island but navigational obstacles prevented us from getting near enough to receive a signal. Oystercatchers were found at Marsh Island at higher tides when Bird Shoal was mostly under water and at lower tides they were only located at Bird Shoal. Bird Shoal may be a more desirable roost site, thus used when available because it is closer to diurnal roosts and foraging sites and it lacks vegetation that can hide predators and limit shorebird visibility (Rogers 2006). We suspect that our focal birds were not foraging at night, at least not on oysters, since oystercatchers were only found at Marsh Island during tides when reefs were not exposed and Bird Shoal does not have oyster reefs. Eurasian Oystercatchers normally forage at night and need to do so because gut processing constraints put a ceiling on the amount of food that can be ingested in a single low tide cycle; they may acquire as much food during nocturnal low tides as diurnal low tides (Kersten 1996, Sitters 2000, Zwarts *et al.* 1996). Whether the same factors apply to American Oystercatchers is not known; moreover those that winter in the Cape Romain Region may have less need to feed at night than the Eurasian Oystercatchers studied in NW Europe because the winter day-length they experience is about two hours longer. Further research is needed to determine whether American Oystercatchers forage at night

At night, oystercatchers and other shorebirds were absent from all roost sites on the AIWW. During winter, these diurnal roost sites can contain over 1,400 American Oystercatchers and 13,000 other shorebirds (Dodd & Spinks 2001, Sanders *et al.* 2004). Thus Bird Shoal and Marsh Island are likely to be the nocturnal roost sites for thousands of shorebirds that roost on the AIWW during the day in addition to the thousands that roost on Marsh Island and surrounding areas (Dodd & Spinks 2001). Because of the concentration of waterbirds at these sites, the conservation value of these islands is high and human disturbance should be minimized, especially at night.

The mean distance from the center of the foraging area to Marsh Island (11,563 m) was longer than to the diurnal roost sites (the capture site) (1,583 m). Daytime roosts are often dispersed near foraging grounds but nocturnal roost sites may contain more birds and be situated farther away from prime feeding areas in order to avoid predation by owls (Piersma *et al.* 2006, Rogers 2003, Rogers *et al.* 2006). Sitters *et al.* (2001) documented 80,000 shorebirds on a beaches backed by cliffs and trees in Australia during daytime high tides but found the same beaches to be deserted during high tide at night. Similarly Sitters *et al.* (2001) considered that Red Knots *Calidris canutus* avoided beaches backed by tall sand dunes at night to reduce the risk of predation by such avian predators as Great Horned Owls *Bubo virginianus* and Short-eared Owls *Asio flammeus*. Great Horned Owl pellets collected in Bolinas Lagoon, California contained shorebirds and American Coots *Fulica americana*, which are similar in size to American Oystercatchers (Brisbin *et al.* 2002, Page & Whitacre 1975). Short-eared Owls have been observed hunting near intertidal flats and have been documented eating shorebirds and birds similar in size to oystercatchers (Glue 1972, Page & Whitacre 1975, Piersma *et al.* 2006). Both Great Horned Owls and Short-eared Owls are present in Cape Romain Region (National Audubon Society 2002). Great Horned Owls have been documented killing oystercatchers on the AIWW in the study area during the breeding season while adults are incubating (J. Thibault, pers. comm.). Additionally, shorebirds roost at different sites at night compared to day as a way to escape mammalian predators (Handel & Gill 1992). Mammalian predators have been observed on the AIWW but not on Marsh Island or Bird Shoal (authors' unpubl. obs.) so owl and mammalian presence may explain why oystercatchers roosted farther from the mainland at night than during the day.

Many high tide roosts are necessary to allow full access to foraging grounds (Dias *et al.* 2006) and Cape Romain Region has numerous diurnal roosts near oyster reefs. South Carolina has abundant and healthy oyster reefs that provide forage for oystercatchers. The combination of roost sites (diurnal and nocturnal) and abundant food may explain why this area has historically and presently had a large concentration of oystercatchers (Sanders *et al.* 2004, Sprunt & Chamberlain 1949).

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An American Oystercatcher attacking an oyster, Cape Romain Region, South Carolina, USA, Nov 2008 (photo: F. Sanders).