EFFECTS OF HUMAN ACTIVITY AND PREDATION ON BREEDING AMERICAN

OYSTERCATCHERS

by

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(Under the Direction of J. Michael Meyers and Sara H. Schweitzer)

ABSTRACT

The United States population of American Oystercatchers (*Haematopus palliatus*) is of special concern. Biologists attribute low numbers and reduced reproductive success to excessive predation and human disturbance; however, researchers have not documented nest predators positively and the mechanism by which human presence reduces reproductive success is not well understood. During the 2003 and 2004 breeding seasons, I video-monitored American Oystercatcher nests ($n = 32$) to document causes of nest failure and observed oystercatcher behavioral responses to human activity at Cumberland Island National Seashore. Hatching and fledging success were 45% and 33%, respectively. Predation was the primary cause of nest failure (44% of nests). Pedestrian activity reduced reproductive behavior during incubation. Vehicular activity reduced foraging behavior during brood rearing. Presence of boats did not affect behavior. Oystercatchers were fairly intolerant of pedestrian activity ≤ 137 m of nests during incubation. During brood rearing, oystercatchers reacted to pedestrian activity ≥ 137 m of chicks.

INDEX WORDS: American Oystercatcher, behavior, Cumberland Island, Georgia, *Haematopus palliatus*, human disturbance, predation, reproductive success, shorebirds, time activity budget, video monitoring

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

In 2005, more than 50% of the United States human population lived in coastal

areas, which comprises only 18% of the country's land base (Bookman et al. 1999). This

population is rapidly increasing and may reach 166 million people by 2015 (Bookman et

al. 1999). At 20% per decade, the coastal population of Georgia is growing rapidly as

well (Georgia Coastal Management Program 1997). With this growth comes greater

pressure on sensitive habitats and wildlife, and intensifies the need to quantify the effects

of human activity on natural systems. Armed with this information, biologists can

develop management plans to control and mitigate for human expansion into these areas.

A species that may be particularly vulnerable to human disturbance is the

American Oystercatcher (*Haematopus palliatus*). The large black and white shorebird

(order Charadriiformes) inhabits coastal regions of eastern United States. Increased

human activity in coastal areas may disrupt oystercatchers' foraging and nesting

behavior, and coastal development destroys nesting and foraging habitat, likely

threatening the viability of oystercatcher populations. This shorebird's conspicuous

nature and sensitivity to human disturbance often makes the species important for coastal

conservation efforts.

The American Oystercatcher is one of four shorebirds listed as species of high

priority by the U.S. Shorebird Conservation Plan (Brown et al. 2001). The oystercatcher

is listed as rare in Georgia (Ozier et al. 1999), with an estimated 100 breeding pairs

nesting along the Georgia coast (Winn 2000). In addition, the bird is listed as threatened

in Florida (Below 1996) and is a species of special concern in Alabama (Holliman 1986).

The U.S. Shorebird Conservation Plan specifically calls for research to determine

American Oystercatcher tolerance to human activity and document positively causes of

nest failure. In accordance with these research needs, the goals of this study are to

determine the causes of nest failure of American Oystercatchers on a portion of the

Georgia coast, as well as quantify the effects of human disturbance on behavior during

the breeding season.

LIFE HISTORY

The American Oystercatcher's range includes the Atlantic coast, from

Massachusetts south to Florida, portions of the Caribbean coast, the Gulf coast of Florida

south to Mexico, and occasionally south to Argentina (Nol and Humphrey 1994). The

bird is one of two species in the family Haematopodidae that occur in North America. Its

close relative, the Black Oystercatcher (*H. bachmani*) is found on the western coast of

North America.

The American Oystercatcher's diet varies with range, but consists primarily of

marine bivalves, mollusks, worms and other marine invertebrates that inhabit coastal

intertidal areas. During my studies on Cumberland Island National Seashore (CINS),

Georgia, I observed oystercatchers foraging on American oysters (*Crassostrea virginica*),

stout razor clams (*Tagelus plebeius*), sand worms (*Nereis* spp.), cannonball jellies

(*Stomolophus meleagris*), knobbed whelks (*Busycon carica*), white baby ears *(Sinum*

perspectivum), and Atlantic giant cockles (*Dinocardium robustum*). In addition,

observation of feeding and inspection of stomach contents by others revealed that diet in

the southern part of its range (Virginia to Florida) consisted of soft-shell clams (*Mya arenaria*), razor clams (*Ensis directus*), Atlantic ribbed mussels (*Geukensia demissa*), mole crabs (*Emerita tolpoida*), sea urchins (*Strongylocentrotus* spp.), starfish (*Asterias* spp.), and crabs (Bent 1929, Tomkins 1947, Cadman 1980, Johnsgard 1981, Nol 1989). At CINS, oystercatchers foraged along the receding tide line on the oceanfront beach, bay-side marshes, creek sides, oyster and mussel beds, and occasionally on insects in the dunes (personal observation). Foraging occurs in similar habitats in other parts of its range (Nol and Humphrey 1994). Oystercatchers locate food visually on slightly submerged shellfish beds (Nol and Humphrey 1994), and oystercatchers at CINS often foraged on exposed shellfish beds (personal observation). Upon locating bivalve prey, the oystercatcher thrusts its long, sharp bill into the open valves. Using short stabbing motions, the oystercatcher severs the adductor chain that secures the two valves together, gaining access to the soft interior parts (Nol and Humphrey 1994).

The American Oystercatcher lives at least 17 years (Nol and Humphrey 1994), and possibly as long as the closely related Eurasian Oystercatcher (*H. ostralegus*), which lives 20–40 years (Ens et al. 1996). Pairs are typically monogamous and pair bonding may last the life of the birds (Palmer 1967, Nol and Humphrey 1994). Polygamy and communal nesting, however have been documented in New York (Lauro et al. 1992) and may be attributed to high density nesting and limited availability of nesting habitat.

From limited mark-recapture data, the American Oystercatcher population north of Virginia appears migratory, while populations south of Virginia are short distance migrants or residents (Terres 1980, Humphrey 1990). Flock behavior typically occurs during the non-breeding season, with groups of up to 100 seen in New York before

migration (Johnsgard 1981, Nol and Humphrey 1994). Southward migration occurs in the fall, with peak winter concentrations of oystercatchers in Virginia, North Carolina, and South Carolina (Tomkins 1954, Post and Gauthreaux 1989, Nol and Humphrey 1994, Brown et al. 2005). Northward migration begins in early spring, leaving resident birds behind to breed locally (Tomkins 1954). Based on limited resightings, several individuals that nested on CINS remained there throughout the winter (P. Leary, unpublished data).

American Oystercatchers establish territories soon after reaching breeding grounds in late February to March in the northern range (Virginia-New York) (Nol and Humphrey 1994). At CINS, pairs established territories late March (personal observation). Pairs typically establish territories six weeks before clutch initiation, and rarely as much as three months in advance (Tomkins 1954, Nol and Humphrey 1994). Territory size varies depending on the quality and location of the habitat and ranges from 0.7 pairs/ha (Virginia) to 13 pairs/ha (New York, Lauro et al. 1992). Territories are often contiguous. Pairs compete for high quality territory, resulting in aggressive intraspecific interactions (Nol et al. 1984, Nol and Humphrey 1994). Intraspecific competition was common at CINS, especially on the north end of the island, where presumably, foraging and nesting habitat quality was high (personal observation).

Site fidelity is common, with pairs returning to the same territory for several consecutive years, even nesting in the same location from one year to the next (Tomkins 1954, Nol and Humphrey 1994). Oystercatchers at CINS nested among Wilson's Plover (*Charadrius wilsonia*) colonies, and despite intense interspecific interactions, close (<50 m) to Least Tern (*Sterna antillarum)* colonies (personal observation). Oystercatchers

also nest among Common Tern (*S. hirundo*), Black Skimmer (*Rynchops niger*), Royal Tern (*S. maxima*), Sandwich Tern (*S. sandvicensis*), and Willet (*Catoptrophorus semipalmatus*) colonies in other regions (Nol and Humphrey 1994, George 2002).

Nest scraping is a part of courtship and occurs several weeks before clutch initiation (Tomkins 1954, Nol and Humphrey 1994). At CINS, pairs searched the back beach, fore dunes and primary dunes for potential scrape sites. Upon finding a location, pairs lightly probed the substrate with their bills (personal observation). If the site was suitable, one member of the pair excavated a scrape by placing its chest on the substrate, and cast sand with its feet. At CINS, scrapes varied in depth and diameter (personal observation). Scrapes are typically 20 cm in diameter and 4–6 cm deep (Nol and Humphrey 1994). Pairs at CINS often made and abandoned many scrapes before choosing a nest site, which confirms Tomkins' (1954) observations (personal observation). When pairs select a nest, they may line the nest with debris collected in or around the nest (Nol and Humphrey 1994). At CINS, pairs constructed linings of shell fragments, vegetation and wrack material, although not all nests were lined (personal observation).

At CINS, nests sites occurred on back beach, fore and primary dunes; however, I found two nests on a high secondary dune ridge, in 2003 and 2004, at the same location. Nests were usually visible from the beach, although dunes or other debris obstructed some. Nests were on slightly elevated areas free of vegetation, or occasionally near *Ipomoea* spp. and *Spartina* spp. Frequently, nests were among scattered debris (personal observation). Other biologists documented that nest site selection was variable, but commonly occured in sparse vegetation (23–50% cover; *Ammophila* spp., *Spartina* spp.,

5

or *Solidago sempervirens*), on open sandy beaches and dunes well above the high tide line (Bent 1929, Tomkins 1954, Rappole 1981, Lauro and Burger 1989, Shields and Parnell 1990, Nol and Humphrey 1994). In the northern range (New York and New Jersey), oystercatchers often nest in marshes, presumably because human disturbance prevents them from nesting on traditional sandy beach nesting sites (Lauro et al. 1992). A recent study found oystercatchers nesting in marsh habitats in Georgia as well (George 2002). My observations confirmed previous findings that oystercatchers construct slightly elevated nests with at least 180 degrees visibility (Bancroft 1927, Bent 1929). Nest elevation is positively correlated with reproductive success (Lauro and Burger 1989). Distance to nearest conspecific nest depends on habitat, but typically ranges from 124–190 m (Nol and Humphrey 1994).

Clutch initiation at CINS began in late March to early May (personal observation). In other areas of Georgia, clutch initiation occurred in late March and peaked in late April (George 2002). Farther north, first clutch initiation may be as late as May (Nol and Humphrey 1994). Clutch size ranges from two to four eggs, most commonly three (Baicich and Harrison 1997). At CINS, clutch size was 2.5 ($n = 32$, CI = 2.3–2.7; this study), which is similar to previous findings in Georgia (Corbat 1990, George 2002). In Virginia, clutch size was 2.6 ($n = 294$, Nol et al. 1984)).

At CINS, oystercatchers laid eggs in 1–2 day intervals; with incubation beginning immediately after the first egg was laid (personal observation). In contrast, Nol and Humphrey (1994) reported that incubation begins after the second egg is laid. Pairs incubated nearly 100% of the time at CINS (personal observation). Females incubate most frequently (Nol 1985). Incubation averaged 29 days at CINS (this study), longer

6

than previously documented (28 days, Tomkins 1954; 24–27 days, Baicich and Harrison 1997). Pairs replaced lost clutches within two weeks at CINS and renested up to two times, into late July (personal observation). Clutch size decreased with successive renests, confirming findings by Nol et al. (1984).

Hatchlings were precocial and remained at the nest for only 1–2 days at CINS (personal observation). They were able to stand and run short distances within hours of hatching. Adults brooded chicks that were <10 days old, although chicks attempted to brood until much older. Both sexes fed young by transporting prey from foraging grounds, by regurgitating food eaten on foraging grounds, or, with older chicks (>3 weeks), by bringing whole shellfish to open in front of the chick. When chicks were young (<2 weeks), one adult guarded the chicks on the breeding ground while the other foraged elsewhere. As the chicks aged, the adults left the chicks alone while they foraged. While adults were away, chicks usually stayed concealed among debris, although as they aged, they became more active in the absence of adults. Older chicks foraged among dune vegetation, presumably for insects (personal observation).

Although fledging occurs 35 days after hatching, young may be dependent on adults for food for up to 60 days, likely due to the difficulty of opening prey (Nol and Humphrey 1994). At CINS, the young remained with adults after fledging, at least until mid-August (personal observation). Young adults do not begin breeding until three to four years old, although second-year oystercatchers will pair, defend territories and excavate scrapes (Tomkins 1954, Palmer 1967, Cadman 1980, Johnsgard 1981).

Studies indicate that reproductive success is low, especially in Georgia. In the 1980s, hatching success was 6% ($n = 32$, Corbat 1990). In the 2000s, hatching and

fledging success was 15% and 7%, respectively (*n* = 209, George 2002). Greater

fledging success was documented in Florida (57%, *n* = 58; Toland 1999). Hatching

success of 14% (*n* = 114) was documented in Virginia (Nol 1989). Although

reproductive success is typically low, American Oystercatchers are long lived, so low

reproductive rates may be sufficient to maintain the population (Davis 1999).

Biologists attribute American Oystercatchers' low reproductive success to several

sources. Eggs and chicks fall prey to raccoons (*Procyon lotor*), feral cats (*Felis cattus*),

red foxes (*Vulpes vulpes*), minks (*Mustela vison*), gulls (*Larus* spp.), and crows (*Corvus*

spp.) (Nol 1989, Corbat 1990, Nol and Humphrey 1994, Davis et al. 2001). In Georgia,

predation and flooding from high spring tides and storms were the most frequent causes

of nest failure (George 2002). Nests failed in North Carolina from similar causes (Davis

et al. 2001). In the same region, predators such as feral cats and raccoons were more

abundant in areas with human activity (Davis et al. 2001). Human disturbance may

increase mortality by flushing birds from nests, making eggs vulnerable to predators as

well as hyper- and hypothermia (Rappole 1981, Toland 1999). On Little Cumberland

Island, Georgia, vehicular traffic from residents and all-night surveys for loggerhead sea

turtle (*Caretta caretta*) nests may cause nest failures and chick deaths (Rappole 1981).

STATUS AND CONSERVATION

The range and abundance of American Oystercatchers before 1900 remains

unknown, but early accounts suggest that the bird nested along the Atlantic Coast, from

Florida, north to Labrador (Audubon 1835; Forbush 1912, 1925; Bent 1929; Griscom and

Snyder 1955). Unrestricted egg collecting, market hunting, and increased human activity

in coastal areas devastated oystercatcher populations along the Atlantic Coast in the late

nineteenth and early twentieth centuries (Richards 1890, Bent 1929). The northern extent of the oystercatcher's range receded south to Virginia and they were considered scarce throughout the mid-Atlantic and southern states (Forbush 1912, Erichsen 1921, Bent 1929, Sprunt 1954).

The Migratory Bird Treaty Act of 1918 significantly reduced direct human impact, after which oystercatchers began to recover. By the 1960's, oystercatchers were once again present as far north as New York (Stewart and Robbins 1958, Post 1961, Post and Raynor 1964, Leck 1984, Zaradusky 1985). By 1979, 18 pairs were nesting in Massachusetts, and by 1986, 42 pairs were nesting along the state's coast (Viet and Peterson 1993, Nol and Humphrey 1994).

In 2004, the estimated United States wintering population was $10,971 \pm 298$ (Brown et al. 2005) and breeding numbers may be declining in the Carolinas and Virginia (Davis et al. 2001). In 1981, the estimated Georgia breeding population was 70 pairs, about half to a third of the state's carrying capacity (Rappole 1981). In 2000, the population estimate increased to 100 breeding pairs (Winn 2000). Low numbers in Georgia have been attributed to low reproductive success caused by excessive predation and human disturbance (Rappole 1981). A recent decline in the Florida oystercatcher population has been attributed to increased human populations in coastal areas (Below 1996, Toland 1999). Wide beaches with well-developed dune complexes are preferred oystercatcher nesting habitat and are also used heavily by humans. Disturbance from people, pets, and vehicle traffic on beaches may result in direct nest destruction or may be causing adults to flush from nests, indirectly causing failure as well.

STUDY OVERVIEW

I planned this study based on research objectives of the U.S. Shorebird Conservation Plan (Brown et al. 2001), concerns of the Georgia Department of Natural Resources, and the needs of CINS. First, I estimated daily survival rates of eggs and chicks and calculated apparent reproductive success on the oceanfront beach of CINS. I accomplished this by using video monitoring equipment to continuously view nests located during beach surveys. Second, I determined causes of nest failure in the egg and hatchling stages by using video monitoring equipment. Third, I estimated disturbance frequency and duration (primarily relative to activities of humans) and their effects on oystercatcher behavior. I collected time activity data on adults and nestlings, as well as numbers and locations of pedestrians, vehicles, and boats within close proximity of nests during the observation period. I correlated time activity data to observed intrusions to account for abnormal behavior or possible failures caused by lack of incubation or protection of eggs. Finally, I quantified oystercatchers' threshold of tolerance to disturbance by subjecting incubating adults to multiple forms of disturbance, at varying distances. I used distance at which birds moved away from nests to quantify a tolerance to various forms of disturbance. Finally, based on the results of this study, I provided recommendations for the management of American Oystercatchers at CINS.

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CHAPTER 2

A SIMPLE, INEXPENSIVE VIDEO CAMERA SETUP FOR THE STUDY OF AVIAN

NEST ACTIVITY[1]

ABSTRACT. Time-lapse video photography has become a valuable tool for avian nest

activity and predation data collection; however, commercially available systems are

expensive (>$4,000/unit). We designed an inexpensive system to identify causes of nest

failure of American Oystercatchers (*Haematopus palliatus*) and assessed its utility at

Cumberland Island National Seashore, Georgia. We successfully identified raccoon

(*Procyon lotor*), bobcat (*Lynx rufus*), American Crow (*Corvus brachyrhynchos*), and

ghost crab (*Ocypode quadrata*) predation on oystercatcher nests. Other detected causes

of nest failure included tidal overwash, horse trampling, abandonment, and human

destruction. System failure rates were comparable with commercially available units.

Our system's efficacy and low cost (<$800) provided useful data for the management and

conservation of the American Oystercatcher and would benefit other studies of nesting

species.

KEY WORDS: American Oystercatcher, Georgia, *Haematopus palliatus*, nesting behavior,

nest failure, predator identification, video surveillance

INTRODUCTION

Time-lapse video monitoring documents birds' activities at nests and causes of

nest failure with minimal disruption to the nest site or adults (Thompson et al. 1999, Pietz

and Granfors 2000, Stake and Cimprich 2003, Renfrew and Ribic 2003, Hoover et al.

2004). Commercially available video monitoring systems, however, can cost >$4,000

per unit, often making multiple video system projects prohibitively expensive. The

development of an inexpensive video system would permit greater use, promoting further

investigation into avian nesting ecology and causes of nest failure. Researchers have

described several "home-built" video systems (Granfors et al. 2001, Sanders and Maloney 2002, Hoover et al. 2004); however, these require at least daily maintenance and may not be suitable for the oceanfront beach environment.

In 2003, we began a two-year study on the effects of disturbance and predation on the reproductive success of beach nesting American Oystercatchers (*Haematopus palliatus*) at Cumberland Island National Seashore (CINS), Georgia. To meet our financial objectives and goal of monitoring every nest, we required a video monitoring system that would cost <$1,000, record nest activity at a minimum of 1–2 frames per second, continuously for at least 48 h, and be secure from vandals and typical environmental conditions.

METHODS

We designed a video system consisting of a black and white, infrared camera and a time-lapse recorder, powered by a 12-volt deep cycle battery (Figures 2.1 and 2.2) for use on the oceanfront beach of CINS. This beach is typical of those found on barrier islands in the Southeastern United States, although human development is low. At 28 km in length, the beach is used daily by tourists, residents, and National Park Service employees.

We used Sony 3.6-mm, waterproof, black and white, infrared cameras, approximately 6.3 cm in diameter and 6.6 cm in length (approx. $130). Integrated infrared light emitting diodes (LED's) provided illumination at low light levels, allowing us to monitor nests 24 h/day. We secured the camera to a short wooden stake using an adjustable mount provided by the camera supplier. To provide protection against adverse conditions, we shielded each camera with a plastic bottle (Figure 2.2). The handle and

17

mouth of the bottle were removed and sand was glued with a spray adhesive to the exterior of the bottle for camouflage.

We used Intelligent 12-volt DC, 960-h time-lapse recorders. This recorder (approx. $400) could be set to several recording speeds (frames/s), providing 8–1,288 h of recording time on a single T-160 VHS tape. We set the recorders to record 2.86 frames/s, which was sufficient to capture short duration avian predations, while providing 168 h of continuous recording. We waterproofed the recorders with 19-liter plastic buckets. We drilled a small hole at the base of the bucket for the video and power cables and sealed the hole with silicone caulking. The recorder was secured in the bucket with foam packing material (Figure 2.1). To reduce operating temperature, we buried the bucket and recorder 2–3 cm under the sand.

We sought 48 h of continuous run time to minimize disturbance to nesting birds. We used 12-volt, 200-amp-h marine deep-cycle batteries (approx. $65), to power the equipment for at least 68 h. Two batteries were required per setup; one to power the equipment while the other charged.

Although cameras were rated to record to a distance of 10 m in zero light, the infrared light dispersed quickly outdoors. We placed each camera 1.5–2 m from a nest to provide sufficient illumination (Figure 2.2). Each camera was connected to a recorder via an 18.3-m, RCA, audio/video and power cable (approx. $30), which was buried 2–3 cm. The recorder and battery were placed 18 m from the camera. We placed the battery in a plastic bag, next to the recorder, and partially buried it. The battery was replaced every 60 h and the tape was replaced every 120 h. We used a small, battery-powered,

black and white television (approx. $40) to properly align the camera's field of view and set the recorder.

RESULTS

Cost of the camera, recorder, two batteries and other supplies totaled <$800 per video system (2002). At this price we were able to purchase 10 systems that effectively monitored 32 oystercatcher nest attempts in 2003 and 2004 at CINS. We recorded >15,000 h of nest activity and documented 20 nest failures. We failed to record 2 of the 20 nest failures because of battery failure. Battery failure and overheating were the primary causes of equipment failure; however equipment failure did not usually result in missing a predation event. Other causes of equipment failure included human tampering and horse trampling.

Camera installation resulted in no nest abandonment. Camera installation and battery change caused the incubating bird to stand and walk from the nest, but our activities at each nest were limited to early mornings and evenings (before 0800 and after 1800), during moderate weather conditions, to minimize adverse impacts on eggs. Initial setup of the system averaged 12 min. Battery and tape change required 7 min on average. Birds returned to incubate typically within 1–2 min after departure from the nest site. Predation was the most common cause of nest failure (13 of 18 failures). We identified 3 egg predators: raccoon (*Procyon lotor*, $n = 9$), bobcat (*Lynx rufus*, $n = 3$) and American Crow (*Corvus brachyrhynchos*, $n = 1$). One chick was depredated by a ghost crab (*Ocypode quadrata*) shortly after hatching. Other causes of nest failure included tidal overwash ($n = 1$), horse trampling ($n = 1$), abandonment ($n = 2$), and human destruction ($n = 1$).

DISCUSSION

We recorded 32 oystercatcher nesting attempts with only minor problems. Early in the first season, recorders tended to overheat and shut down during midday. Hence, we buried the buckets 2–3 cm under the sand. This solved the overheating problem, but increased the time necessary to replace the VHS tape by ca. 30 s. The plastic bottle shielded the camera from the heat of direct sunlight. Cameras came into contact with moisture daily, but the cameras were sealed effectively against moisture. We experienced no camera malfunction.

The position (10 cm above ground) and orientation of the camera resulted in a few difficulties. The angle from the camera to the nest was shallow, limiting view into the nest and making chick observation difficult. Because the camera was close to the ground, rainfall splashed sand onto the camera lens, sometimes obstructing the field of view. A solution to both problems would be to elevate the camera, but this may make the camera difficult to conceal from pedestrians.

Heat, humidity, sand, and salt water, found in abundance in the oceanfront beach environment, are potential causes of electronic equipment failure. Our camera setup functioned reliably under the environmental conditions encountered with few equipment failures. Equipment failure rate during nest failure events was 10% (2 of 20), similar to studies using commercially available equipment. Thompson et al. (1999) and Brown et al. (1998) reported 11% (3 of 28) and 7% (2 of 27) unrecorded failures, respectively.

Because of low sample size, we made no attempt to discern an effect of the camera on predation rate or nesting activity using unrecorded control nests. We were concerned that a faint red glow emitted by the infrared LED's would be seen by the

20

nesting birds or attract predators to the nest. Although we were unable to test this hypothesis, Sanders and Maloney (2002) found that a glow emitted by their cameras had no effect on predation rate ($\chi_1^2 = 0.22$, $P = 0.64$). Most researchers have found that predation rates at video monitored nests were not different from those at nests without video equipment (Brown et al. 1998, Pietz and Granfors 2000, Thompson and Burhans 2003, Stake and Cimprich 2003, Renfrew and Ribic 2003). In our study, video equipment and associated activities had no detectable impact on reproductive success, when compared to previous studies without video monitoring in Georgia, North Carolina and Virginia (Nol 1989, Davis et al. 2001, George 2001). Although 2 nests were abandoned, no nests were abandoned within 20 d of camera installation and nesting activity appeared to return to normal within minutes after installation, suggesting that the camera had little or no effect on the nesting birds' activity. Some researchers have found increased abandonment rates on video monitored nest and suggest caution when using cameras (Brown et al. 1998, Renfrew and Ribic 2003).

Because our video equipment coped well with environmental extremes encountered at CINS, we believe that the system would function reliably in most settings and may be adapted for many applications. Using the adjustable mount, cameras may be secured to a clamp for attachment to a branch or pole that would allow for monitoring of canopy, and shrub nesters. Ground nesters and grassland species may be monitored using the same staking technique we used. Monitoring of smaller species or nests in dense vegetation may require that the camera be closer to the nest than out setup (1.5–2 m). It is unknown how camera proximity may affect the rate of nest abandonment by other species. Camouflage with local vegetation or debris, or use of a smaller camera may be

less obtrusive. Smaller cameras are available at a slight increase in price (approx. $60–70).

Evidence from our study and current literature suggests that with careful application, cameras have few negative impacts on reproductive success, predation rates, and nesting activity. With this equipment, we successfully identified previously undocumented causes of nest failures (e.g., horse trampling and crab predation on nestlings) and collected valuable data on nesting activity with relative ease and at a cost of <25% of commercially available equipment (Thompson et al. 1999). Sanders and Maloney (2002) suggest that video equipment be used for more than just identifying nest predators. They encourage research designed with sample sizes large enough to quantify the relative impacts of causes of mortality in the ecosystem. With our cost effective video system this research is possible.

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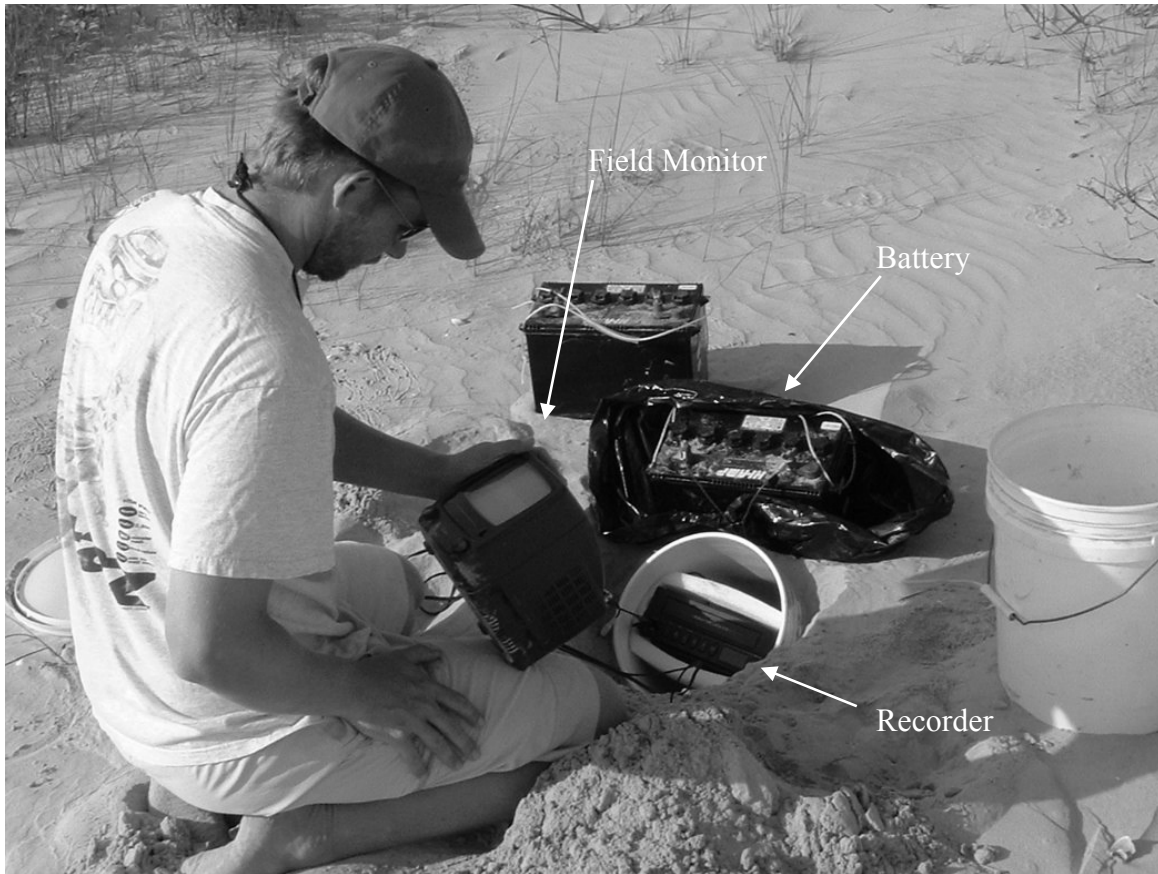
Figure 2.1. Recorder and battery used to record avian nest activity. Recorder and 19-liter bucket were buried 2–3 cm in the sand and battery was concealed in plastic bag. A portable television was used to orient camera view and setup recorder

Figure 2.2. Each camera was mounted on a wooden stake, placed approximately 1.5–2 m from a nest, and protected by a cutout plastic bottle. An 18.3-m cable buried 2–3 cm in the sand substrate connected each camera to a recorder and battery

CHAPTER 3

NEST FATE AND PRODUCTIVITY OF AMERICAN OYSTERCATCHERS,

CUMBERLAND ISLAND NATIONAL SEASHORE, GEORGIA[1]

ABSTRACT. The American Oystercatcher (*Haematopus palliatus*) is listed as a species of high priority by the U.S. Shorebird Conservation Plan and is state-listed as rare in Georgia; however, biologists have not focused on identifying the causes of egg and hatchling losses. In 2003 and 2004, continuous video monitoring was used to document reproductive success of American Oystercatchers and identify causes of nest failure at Cumberland Island National Seashore, Georgia. The modified Mayfield method and program CONTRAST were used to determine and compare survival of eggs and nestlings. Eleven pairs made 32 nest attempts during two seasons. Nine pairs were successful, fledging 15 chicks. Daily survival of clutches was 0.973 (95% CI = 0.960–0.987) for 2003, 0.985 (95% CI = 0.974–0.995) for 2004, and 0.979 (95% CI = 0.970–0.987) for combined years. Daily survival was greater on the north end, than on the south end of the island ($\chi_1^2 = 7.211$, $P = 0.007$), due to lower rates of nest predation and lower human disturbance. Eighteen of 20 nest failures during the egg stage and one of eight chick losses were documented. Predation accounted for 14 nest failures. Egg predators included raccoon (*Procyon lotor*, $n = 9$), bobcat (*Lynx rufus*, $n = 3$), and American Crow (*Corvus brachyrhynchos*, $n = 1$). A ghost crab (*Ocypode quadata*) preyed on one chick. Other causes of nest failure were tidal overwash ($n = 1$), horse trampling ($n = 1$), abandonment ($n = 2$) and human destruction ($n = 1$). Predator control may be an effective means of increasing reproductive success on the south end of the island. The north of the island has one of the highest reproductive rates reported along the Atlantic Coast. Therefore, managers should place priority on conserving this area from human and predator encroachment.

KEY WORDS: American Oystercatcher, Georgia, *Haematopus palliatus*, human disturbance, predation, reproductive success, shorebirds, video monitoring

INTRODUCTION

The American Oystercatcher (*Haematopus palliatus*) is one of four high priority

shorebirds listed by the U.S. Shorebird Conservation Plan (Brown et al. 2001) and is state-listed

as rare in Georgia (Ozier et al. 1999). The estimated eastern U.S. wintering population was

10,971 ± 298 individuals in 2005, which is less than the minimum for high priority status (Brown

et al. 2005). Small population size, nesting habitat preference for frequently disturbed Atlantic

oceanfront beach, and naturally low annual fecundity are likely causing population declines (Nol

and Humphrey 1994, Davis et al. 2001). Although biologists have investigated oystercatcher

reproductive ecology on the eastern U.S. coast (Nol 1989, Corbat 1990, Davis et al. 2001,

George 2002, McGowan 2004), we lack a clear understanding of population and reproductive

trends.

Shorebird biologists have identified causes of nest failure by examining signs de facto

(Nol 1989, Corbat 1990, Davis et al. 2001, George 2002, McGowan 2004). There is evidence of

egg and chick predation by raccoons (*Procyon lotor*), domestic cats, red foxes (*Vulpes vulpes*),

mink (*Mustela vison*), gulls (*Larus* spp.), and crows (*Corvus* spp.) (Nol 1989, Corbat 1990, Nol

and Humphrey 1994, Davis et al. 2001). Human disturbance may increase predator-related

mortality by flushing adults from nests, thereby exposing eggs and providing a nest location cue

for predators (Skutch 1949). Unattended nests also make eggs vulnerable to hyper- and

hypothermia (Rappole 1981, Toland 1999). Flooding from high spring tides and storms is a

common cause of nest failure as well (Nol 1989, Corbat 1990, Davis et al. 2001, George 2002,

McGowan 2004).

With the exception of a few chance sightings, most nest fate data are based on

interpretation of signs 1–4 days following nest failure. Determining the cause of failure by

interpreting signs can be difficult and misleading. Predator tracks and other sign left in soft sand

can be diffuse and ephemeral. Many species share similar patterns of nest predation, which

makes identification difficult (review by Lariviere 1999). A predation event may attract other

predators to a nest making identification of the original predator difficult or impossible

(Lariviere 1999). Weather events, such as wind and rain also eliminate evidence of predators.

The difficulty of identifying nest predators of American Oystercatchers was evident in

recent studies that failed to identify causes for almost half of nest failures. In North Carolina,

biologists did not identify nest predators for 47% of failures ($n = 213$, Davis et al. 2001). In

Georgia, recently, biologists were unable to determine the cause of 40% of clutch losses ($n =$

209, George 2002). Because biologists have not focused on identification of causes of nest, egg,

and hatchling losses, studies are needed to identify these causes specifically to understand factors

contributing to low productivity of American Oystercatchers. Our objectives were to estimate

reproductive rates of American Oystercatchers at Cumberland Island National Seashore (CINS)

and determine the causes of nest failure using video monitoring equipment.

<div align="center">STUDY AREA</div>

We conducted field investigations at CINS, a 14,736-ha barrier island on the southeastern

Georgia coast (30°N, 81°W). The oceanfront beach of the northern (4 km, North End, Figure

3.1) and southern portions of the island (11 km, South End) were characterized by well-

developed back beach and dune systems that provided nesting habitat for several avian species,

including Least Terns (*Sterna antillarum*), Gull-billed Terns (*S. nilotica*), Wilson's Plovers

(*Charadrius wilsonia*), and 10–12 pairs of American Oystercatchers. Heavy erosion from wind

and wave action truncated dunes in the middle portion of the island (13 km), subsequently the

area provided little nesting habitat. The South End of the island was wide (2 km) and distance

from primary dune to interdune scrub ranged from approximately 200–300 m. The North End

was a narrow peninsula bounded by the Atlantic Ocean to the east and Christmas Creek to the

north and west. Interdune habitat and maritime forest formed the southern border of the North

End.

Potential nest predators on CINS included bobcat (*Lynx rufus*), raccoon, mink, nine-

banded armadillo (*Dasypus novemcinctus*), feral hog, white-tailed deer (*Odocoileus virginianus*),

American alligator (*Alligator mississippiensis*), feral horse, and several avian species (Johnson et

al. 1974). Feral hogs have been trapped or hunted periodically since 1975. By 2004,

approximately 4,800 hogs had been culled (J. Fry, CINS, personal communication). Raccoon

control was sporadic and limited to nuisance individuals and those that posed a direct threat to

loggerhead sea turtle (*Caretta caretta*) nests. National Park Service (NPS) employees removed

<30 raccoons from the island in 2003 and 2004 (W. E. O'Connell, CINS, personal

communication).

Because NPS facilities were located primarily on the South End, most tourist activity

occurred there. Forms of human disturbance on the oceanfront beach included pedestrian, boat,

and vehicle (all-terrain vehicles, pick-up trucks, sport utility vehicles) traffic. The North End,

designated as wilderness by NPS, was free of most human disturbance, except NPS employees,

long distance hikers, and residents who had beach driving permits (*n* = 326, C. Gregory,

GADNR, personal communication).

METHODS

Daily surveys along the beachfront were conducted to locate breeding pairs and nests

during the 2003 and 2004 breeding seasons (Mar–Aug). Surveys were from vehicle and on foot.

Nest locations were recorded using the global positioning system (GPS) (Garmin GPS 12), nests

were marked with a small florescent marker (paint stirrer) placed approximately 3 m seaward of the nest, and number of eggs present was recorded. Video monitoring equipment was placed at each nest site within 24 h of locating it. This equipment consisted of a miniature black and white infrared camera (1.5–2.0 m from nest) and a time-lapse recorder (19–20 m from nest), powered by a 12-volt deep-cycle battery (Sabine et al. 2005). Batteries were replaced every 60 h and VHS tapes were replaced every 120 h. During each battery change, nests were checked for missing or damaged eggs. Activity at the nest site was limited to morning and evening hours (before 0800 h or after 1800 h), moderate climatic conditions, and to 7 min to minimize impact to eggs or chicks.

On days when no battery or tape change was necessary, nests were monitored from a distance (approx. 50 m), minimizing disturbance to incubating birds. When a nest failed, video monitoring equipment was removed and the tape was reviewed to identify the cause. If eggs hatched, video equipment was left in place until chicks left the nest (2–3 d). Chicks were monitored daily with binoculars or spotting scopes until failure or fledging. If a chick was lost, the area was searched for carcasses (100 m radius).

Hatching and fledging success were calculated as a percentage of total nest attempts (apparent success) and daily survival of clutches and chicks was estimated using the modified Mayfield method (Mayfield 1961, 1975; Bart and Robson 1982; Hines 1996). We compared daily survival estimates between nesting stages, years, and North and South Ends using the program CONTRAST (Hines and Sauer 1989). Because of low sample sizes, we pooled data between years and locations to compare daily survival estimates between nesting stages. We made year and location comparisons based on daily survival estimates calculated from combined nesting stages, and were considered different if $P < 0.05$.

RESULTS

PRODUCTIVITY

Eleven breeding pairs established territories in 2003 and 10 pairs established in 2004 (Table 3.1). In 2003, pairs made 19 nest attempts. Six nest attempts were renests, and two were second renests. Six (32%) hatched at least one egg. In 2004, 10 pairs made 13 nest attempts. Six (46%) hatched at least one egg. Seven and three pairs made one and two attempts, respectively. Combined years apparent hatching success was 38%. Mean clutch size was 2.5 eggs per nest ($n = 32$, mode = 2.00, CI = 2.3–2.7). Mean incubation period, calculated using nests with known initiation dates, was 29.1 days ($n = 9$, CI = 27.3–30.9). For two years, 15 chicks fledged from nine clutches (28%); six from four clutches (21%) in 2003 and nine from five clutches (38%) in 2004. All pairs that fledged a chick did so on the first nesting attempt. Three pairs that hatched at least one egg did not fledge chicks.

Combined years daily survival estimate during incubation was 0.973 ($n = 32$, CI = 0.961–0.985) and 0.991 ($n = 12$, CI = 0.982–1.00) for brood rearing. Daily survival estimates between stages were different ($\chi_1^2 = 5.671$, P < 0.02). Based on a mean incubation period of 29 days, the probability of at least one egg in a clutch hatching was 0.452. Assuming chicks fledged within 35 days (Nol and Humphrey 1994), survival from clutch initiation to fledging was 0.329.

Combined nesting stages daily survival estimates were 0.973 (95% CI = 0.960–0.987) for 2003 and 0.985 (95% CI = 0.974–0.995) for 2004, and were not different ($\chi_1^2 = 1.724$, n.s.). Combined estimated daily survival for both years was 0.979 (95% CI = 0.970–0.987). We found 19 nests on the South End and 13 nests on the North End for combined years (Figure 3.2). Daily survival estimates for the North End (0.990, 95% CI = 0.982–0.998) and the South End (0.965, 95% CI = 0.948–0.981) were different ($\chi_1^2 = 7.2$, P < 0.01).

Twenty-three (72%) of 32 nest attempts failed. Twenty failed during the egg stage and three during the hatchling stage. We documented 18 of 20 (90%) failures during the egg stage (Sabine et al. 2005). Chicks were difficult to video monitor because they left the nest site 24–48 h after hatching; consequently, we only documented one chick loss on videotape.

Predation was the primary cause of nest failure, accounting for 13 losses during the egg stage and one chick loss. Egg predators included raccoon (*Procyon lotor*, $n = 9$), bobcat (*Lynx rufus*, $n = 3$), and American Crow (*Corvus brachyrhynchos, n = 1$). One chick was preyed on by a ghost crab (*Ocypode quadrata*), just after hatching. Except for one predation by a crow, all occurred at night. Other causes of nest failure included tidal overwash ($n = 1$), horse trampling ($n = 1$), abandonment ($n = 2$) after 34 and 35 d of incubation, and destruction by a child (Figure 3.3).

Rate and cause of nest failure was variable by location. Mammalian predation was more frequent on the South End. Seven raccoon and three bobcat predations occurred on the South End, compared with only two raccoon predations on the North End. Predation by other species occurred only on the North End (ghost crab, American Crow). Other causes of nest failure, including horse trampling, tidal overwash, and human destruction also only occurred on the South End.

DISCUSSION

PRODUCTIVITY

Mean clutch size on CINS was similar to clutch sizes documented other studies. Clutch sizes in other regions of Georgia were relatively small (2.25, $n = 32$, Corbat 1990; 2.00, $n = 209$ George 2002, respectively). Studies in both Florida (Toland 1999) and Virginia (Nol et al. 1984) documented a mean clutch size of 2.6 ($n = 58$, $n = 257$, respectively).

Hatching (32%, 2003; 46%, 2004, apparent nest success) and fledging (21%, 2003; 38%, 2004) success at CINS was high, compared with other studies in Georgia. In the 1980's, only 2 of 19 (6.3%) nests hatched at least one egg with 13 nest outcomes known (Corbat 1990). In the 2000's, 15% apparent hatching success ($n = 209$), and 7% apparent fledging success was found in Georgia (George 2002). In Florida, apparent fledging success was higher (57%, $n = 58$; Toland 1999). Hatching success of 14% ($n = 114$) was documented in Virginia (Nol 1989).

Hatching and fledging success at CINS differed between the North and South Ends of CINS. In North Carolina, hatching success was variable also, ranging from 4–23% ($n = 996$, McGowan 2004), as was hatching success in Georgia (0–30%, $n = 209$, George 2002). High variability in reproductive success among oystercatchers appears to be common, and indicates that local factors strongly influence reproductive success (e.g., predation, human activity), even within a single island setting. It is unclear how current reproductive rates are affecting population trends, although high annual survival rates and long life spans may help to sustain populations with low and variable reproduction. Occasional spikes in reproductive success may be sufficient to sustain or even increase a population (Davis 1999); however, historical records indicate that the population is in decline south of Virginia (Davis et al. 2001).

NEST FATE

Mammalian predation was the primary cause of nest failure at CINS and influenced reproductive success between North and South Ends. All predations on the South End were by mammals. In North Carolina, 77% of nest failures were due to predation and raccoons were the primary mammalian predator, based on interpretation of signs at the nest site (Davis et al. 2001). Bobcats were a previously undocumented American Oystercatcher nest predator. Bobcats, however, were restored to CINS in 1988 (Baker et al. 2001). Other biologists documented a

negative correlation between predator communities and reproductive success. In North Carolina, daily survival of nests increased following gray fox (*Urocyon cinereoargenteus*) control on Hatteras Island, North Carolina (Z = 3.2, *P* < 0.01, McGowan 2004). Also, lower reproductive success was found on islands with known raccoon populations compared to those without (Z = 7.0, *P* < 0.001).

Differences in predation rates and sources may be affected by differences in environmental and anthropogenic influences between the North and South Ends. Primary predators on the South End were raccoons and bobcats, both of which could easily travel the short distance from the forested island interior to nesting sites (200–300 m). Human presence may maintain higher mammalian predator populations on the South End as well (Prange et al. 2003). Raccoon sightings and sign were greater in areas of increased human activity in North Carolina (Novick 1996, Davis et al. 2001). Raccoon and bobcat signs appeared to be more abundant around areas of frequent human activity at CINS (J. B. Sabine, personal observation). Access to nests on the North End by mammalian predators may have been restricted because of the distance from forest to nesting sites (1–2 km). Predation on the North End was by species that are commonly found on the beach (ghost crab, American Crow) regardless of proximity to forested habitat.

In areas of frequent human activity, we observed commonly pedestrians in close proximity to nests, causing the adults to walk off nests. Pedestrians rarely noticed oystercatcher alarm calls and display activities (J. B. Sabine, personal observation). Human presence in the dunes not only resulted in nest failure, but also caused the incubating adult to temporarily abandon the nest, exposing eggs and chicks to temperature extremes and greater risk of predation. One nest, located in an area of frequent pedestrian traffic was abandoned after 35

days of incubation. Examination of the eggs following abandonment revealed partially developed embryos. Adults frequently were observed off the nest when pedestrians were nearby. The cause of failure is unknown; however, we suspect that the nest failed because of thermal stress to eggs caused by a lack of incubation and induced by human disturbance. Regulations to keep people out of the dunes may not be effective and education programs on American Oystercatchers may be helpful in reducing human disturbances.

Overwash rarely caused nest failure at CINS. Although it was documented previously as a primary contributor to nest failure in Georgia, overwash occurs primarily on sandbars and marshes (George 2002). Overwash on barrier islands beaches was rare (14 of 69 nests, George 2002). Several researchers documented flooding as the primary cause of nest failure on low elevation sand spits or marsh habitats as well (Kilham 1979, Nol 1989, Corbat 1990). Nesting at higher elevations reduces the probability of overwash and, after hatching, the dunes provide refuge from predators and high tides (Lauro and Burger 1989). The abundance of high elevation nesting habitat in the well-developed dune system at CINS provided ample nesting habitat out of reach of high tides.

Nest failure by trampling by horse was previously undocumented. Horse activity on the beach as well as multiple near tramplings were observed (J. B. Sabine, personal observation), which suggests that this is a regular source of nest failure from year to year. As much as 23.5% ($n = 17$) of nest failures on Little St. Simons Island resulted from trampling by cattle (Corbat 1990). Feral horses, found on several barrier islands along the East Coast, can be detrimental to the sensitive dune complex. They graze dune forming vegetation and trample dunes, which results in destabilization and erosion of the dune complex (Johnson et al. 1974) and potentially destroys nest of several species of ground nesting shorebirds.

Chick loss was a major source of reproductive failure at CINS, but only one loss was documented at CINS. Gulls and other oystercatchers were observed attacking and stabbing at chicks (J. B. Sabine, personal observation). A Laughing Gull (*Larus atricilla*) killed a chick in North Carolina (McGowan 2004). Radio tracking chicks may be an effective technique to document causes of chick loss.

In areas of high predation rates, predator control increases reproductive success (McGowan 2004); however, this management tool is labor intensive, long-term, and often very expensive. Additionally, in areas of frequent human activity, predator control is difficult to implement safely. Perhaps conservation funds would be better-spent protecting areas that have been documented as areas of high reproductive success, such as the North End of CINS and Egg Island Bar, at the mouth of the Altamaha River in Georgia (George 2002). Funding should be allocated for further research, to monitor annual American Oystercatcher reproduction in these important areas and to identify other areas of high reproductive success for conservation and protection. Use of areas of high reproductive success for recreation purposes may attract predators and disrupt nesting activities, so plans should be made to protect these areas from human disturbance.

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Table 3.1. Hatching and fledging success of American Oystercatchers at Cumberland Island National Seashore, Georgia, 2003 and 2004.

Year	No. of pairs	No. of clutches	No. of clutches that hatched chicks (%)	No. of clutches that fledged chicks (%)	% of hatched clutches that fledged chicks	No. of chicks fledged
North End						
2003	5	6	5 (83)	4 (67)	80	6
2004	5	7	3 (43)	3 (43)	100	6
South End						
2003	6	13	1 (8)	0 (0)	0	0
2004	5	6	3 (50)	2 (33)	67	3
Total		32	12 (38)	9 (28)	75	15

Figure 3.1. Cumberland Island National Seashore, Georgia, and locations of American Oystercatcher nest sites during 2003 and 2004 breeding seasons.

Figure 3.2. Child destroying an American Oystercatcher's nest, Cumberland Island National Seashore, Georgia, 2004. The nest failure was documented by video monitoring equipment.

CHAPTER 4

EFFECTS OF HUMAN ACTIVITY ON BEHAVIOR OF BREEDING AMERICAN

OYSTERCATCHERS, CUMBERLAND ISLAND NATIONAL SEASHORE, GEORGIA [1]

ABSTRACT: Increased human use of coastal areas threatens the United States population of American Oystercatchers (*Haematopus palliatus*), which is considered a species of special concern. Biologists attribute low numbers and reduced reproductive success to human disturbance; however, the mechanism by which human presence reduces reproductive success is not well understood. During the 2003 and 2004 breeding seasons, we studied American Oystercatchers on Cumberland Island National Seashore (CINS). To determine how human activity affected behavior, we examined behavior in the presence and absence of ambient levels of human activity, and correlated responses to documented causes of nest failure using mixed models regression analysis. Proportions of time human activities were present ($\leq$300 m of subjects) during observations averaged 0.14 ($n = 32$, 95% CI = 0.08–0.20). Human activity affected oystercatcher behavior ($P < 0.05$). During incubation, pedestrian activity $\leq$137 m of subjects reduced the proportion of time devoted to reproductive behavior, but pedestrian activity 138–300 m had no effect. Vehicular and boat activities had minimal effects on oystercatcher behavior during incubation. During brood rearing, the effect of pedestrian activity $\leq$137 m was inconclusive, but pedestrian activity 138–300 m increased proportion of time devoted to reproductive behavior. Vehicular activity decreased foraging behavior during brood rearing, but boat activity had no effect. We attributed <10% ($n = 2$) of nest failures to human disturbance. Human related nest failures occurred in areas of greater human activity. We recommend that managers minimize pedestrian activity $\leq$137 m of nests during incubation. During brood rearing, protection from pedestrian activity should be increased to >137 m and vehicular activity should be minimized.

INTRODUCTION

The American Oystercatcher may be particularly susceptible to human activity in coastal areas. As coastal marine specialists, oystercatchers prefer wide beaches with well-developed dune complexes along the Atlantic Coast of North America. Over 50% of the United States human population lives in coastal areas (Bookman et al. 1999). Coastal areas in Georgia have remained relatively undeveloped; however, the human population in coastal Georgia is increasing at a rate of 20% each decade (National Oceanographic and Atmospheric Administration 2003). Biologists attribute low numbers of oystercatchers and population declines in Georgia and Florida to increased human presence in coastal areas (Rappole 1981, Below 1996, Toland 1999). Recent studies suggest the American Oystercatcher population of the Mid-Atlantic states is declining (Mawhinney and Bennedict 1999, Nol et al. 2000, Davis et al. 2001). With a total United States breeding population estimated at 10,971 individuals (Brown et al. 2005), the United States Shorebird Conservation Plan lists the American Oystercatcher as a species of high priority (Brown et al. 2001).

Effects of human activity on American Oystercatchers are not well understood; however, researchers have found that human disturbance can have negative effects on aspects of the reproductive ecology of other species of oystercatchers. Eurasian Oystercatchers (*H. ostralegus*) have reduced fledging success in the presence of human disturbance (Verhulst et al. 2001). Human activities reduced reproductive success and

46

influenced geographical distribution of African Black Oystercatchers (*H. moquini*) in South Africa (Jeffery 1987, Leseberg et al. 2000). Human disturbance and use of coastal areas have been implicated as primary causes of the extinction of the Canarian Black Oystercatcher (*H. meadewaldoi*) (Hockey 1987).

The probability of nest failure is greater among American Oystercatchers in areas of greater human activity (Novick 1996, Davis 1999), but the mechanism by which human presence reduces reproductive success is not clear. One hypothesis states that increased parental activity caused by human presence attracts predators, increasing nest predation rates (Skutch 1949, Martin et al. 2000, Tewksbury et al. 2002). In North Carolina, evidence of mammalian predators was greater in areas of human activity, which could increase predation rates (Davis 1999). Human activity may also reduce nest attendance, making clutches susceptible to thermal stress (Vleck and Vleck 1996).

To understand oystercatcher behavior, we must account for behavioral changes induced by naturally occurring environmental variations. Several environmental factors influence the behavior of American Oystercatchers, e.g., foraging behavior occurs predominantly during falling and low tides (Nol and Humphery 1994); oystercatchers engage in territorial defense with neighboring oystercatchers (Nol 1985); and gular fluttering occurs at high temperatures (Nol and Humphrey 1994). To determine the effects of human activity on American Oystercatcher behavior, we studied oystercatchers in the presence and absence of human activity relative to naturally occurring environmental conditions (tide, temperature, and presence of intraspecific activity). Examining the implications of human activity on behavior may not be indicative of changes in reproductive success or population dynamics (Gill et al. 2001). To address

these concerns, we studied a population of American Oystercatchers for which nest fates were video documented (Sabine et al. 2005).

Our specific objectives were to: (1) compare breeding behavior of a representative population of American Oystercatchers during natural environmental fluctuations with behavior in the presence of human activity, (2) estimate a threshold of tolerance to human activity, and (3) relate effects of human activity to video documented causes of nest failure.

STUDY AREA

We conducted investigations at CINS, a 14,736-ha barrier island off the southern coast of Georgia (30^oN, 81^oW). The northern tip (4 linear km) and southern portion (11 linear km) of the island had a wide sloping beach and well-developed dune complex that provided nesting habitat for several ground-nesting avian species, including Least Terns (*Sterna antillarum*), Gull-billed Terns (*S. nilotica*), Wilson's Plovers (*Charadrius wilsonia*), and 10–12 pairs of American Oystercatchers. Dunes in the central portion of the island (13 linear km) were truncated by heavy erosion from wind and wave action. The southern portion of the island was wide (2 km), with interdune scrub and maritime forest in close proximity to the oceanfront beach (300–500 m). The northern point was a sand spit bounded by the Atlantic Ocean to the east and Christmas Creek to the north and west. Maritime forest bounded the northern end to the south.

Tourists, National Park Service (NPS) employees and volunteers, and island residents used the beach in the forms of pedestrian, boat, vehicle, and all-terrain vehicle (ATV) traffic. NPS facilities were located primarily on the southern half of the island, where most tourist activity occurred. The northern half of the island, designated as

48

Wilderness by NPS, was free of most human disturbance, except occasional NPS employees, tourists with backcountry permits, and residents with beach driving permits ($n = 326$, C. Gregory, GADNR, personal communication). NPS recorded 41,612 recreation visits to the island in 2003 and 38,258 in 2004 (NPS, unpublished data). Unrecorded visitors gained access to the island by boat on the southern beach, which accounted for substantial numbers (10-15 boats/d) (J. B. Sabine, personal observation).

METHODS

We conducted daily surveys along of the beach to locate breeding American Oystercatchers and nests during 2003 and 2004 (Mar–Aug) (Sabine 2005). We recorded nest locations using the global positioning system (GPS) (Garmin GPS 12), marked nests with a small florescent orange stake (paint stirrer placed approximately 3 m seaward of the nest), and recorded number of eggs present. We placed video monitoring equipment at the nest to record activity and causes of nest failure (Sabine et al. 2005).

Within 24 hr of locating a nest, we began observations of the breeding pair. Using spotting scopes and binoculars, we collected data from a blind or vehicle on the beach ($\geq$50 m), or across channels in a boat. Individuals were not banded, so we assumed pairs maintained territories throughout the breeding season.

We divided days into 4 equal time intervals (0600–0859 hr, 0900–1159 hr, 1200–1459 hr, 1500–1800 hr). Because pairs were widely dispersed, it was impossible to collect data on pairs at random; however, we collected data on each pair equally within each time interval and as randomly as possible. We collected 1 hr of observational data during each session, 30 min for each member of the breeding pair. With 2 observers, we observed both members simultaneously for 30 min; if 1 observer was present, we

observed subjects in random succession. We collected data on breeding pairs during incubation until failure or hatching, and during brood rearing until failure or fledging. We assumed fledging occurred 35 d after hatching (Nol and Humphrey 1994).

During the observation period, we recorded instantaneous behavior at 15-sec intervals using a metronome (Wiens et al. 1970, Baldassarre 1988). We recorded 19 behaviors, modified from Nol (1985), based on observations made before initiation of the study. Behaviors (19) were copulate; incubate – sitting or standing directly over nest; maintain nest – placing the chest on nest rim and using scraping motion with feet to deepen the nest or remove debris; brood – sitting or standing directly over chicks with wings partially extended; provision chick – presenting and breaking up food for chicks; preen – using the bill to arrange feathers, remove external parasites, or scratch; bathe – splashing water on wings; stretch; hop – short vertical leap while flapping wings, usually following bathing; shake; fly; walk; forage – using bill to open prey or probing the substrate for prey; drink; rest – standing or sitting with head turned back and bill tucked under wing (bill tuck); sit – sitting or legs bent slightly in crouching position with no bill tuck; vigilance – standing with no bill tuck; alarm – piping display, head bobbing, chasing, being chased, or other agonistic behavior; and out-of-sight – subject bird not directly observable. Simultaneous to collection of behavioral data, we collected data on anthropogenic disturbances in the vicinity (≤ 300 m) of the pair being observed. These data included type of disturbance (pedestrian, vehicle, or boat) and approximate distance of the disturbance from the subject bird. We recorded the two closest disturbances when multiple disturbances were present.

Intraspecific interaction regularly disturbed pairs and occurrence was not uniform in the study area (J. B. Sabine, personal observation). To account for conspecific effects on

behavior, we included extra-pair oystercatchers in the analysis. We did not collect data on other species present on the study site, because other species were always present throughout the study area and interspecific interaction was rare relative to human and intraspecific interactions.

During 2004, we recorded surface temperature from 5 randomly chosen nesting sites and 5 random locations within the oystercatchers' typical nesting habitat (backshore and fore dunes). We housed each temperature data logger in a 15-cm long, 2.54-cm diameter PVC pipe, staked vertically 5 cm above the ground surface. We capped the pipe on top, leaving the bottom open. Data loggers recorded ambient temperature every 5 min throughout the breeding season. We averaged all sets of temperatures to obtain a mean surface temperature for the island. Because we did not record surface temperature in 2003, we obtained temperature data from the nearest weather station (Golden Isles Airport, Brunswick, Georgia). We used linear regression analysis to fit 2004 weather station data to data collected from the beach ($y = 1.061 + 0.989x$, $R^2 = 0.860$, $P<0.0001$). To obtain ambient temperature for 2003, we fitted weather station data for 2003 to this regression.

To assess the distance at which various forms of anthropogenic disturbance induced a behavioral response by incubating oystercatchers, we conducted a disturbance experiment on breeding pairs in 2004. We mimicked forms of disturbance that typically occurred in the area (vehicular, ATV, and pedestrian traffic) by driving or walking by nests, in a line tangential to the nest. For pedestrian disturbance trials, we included 3 distance treatments (20, 40, and 60 m seaward of the nest). For vehicle and ATV disturbance trials, we drove by each nest, immediately below the high water line (approx.

50 m seaward of nests). During each trial we recorded the incidence of displacement

from the nest (incubating bird walked from nest). If displacement occurred, we stopped

and recorded the line of sight distance from our disturbance to the nest, using a laser

rangefinder. We applied multiple trials of each disturbance type and distance to nests,

until hatching or nest failure. We limited trials to once daily per nest and during cooler

conditions. If our disturbance caused displacement, we recorded distance measurements

quickly and left the area immediately, allowing the bird to return to the nest.

The University of Georgia permitted manipulation of birds, Animal Care and Use

Permit No. A2002-10207-cl, as did NPS, Scientific Research and Collecting Permit

Number CUIS-2003-SCI-0002.

STATISTICAL ANALYSIS

We reduced 19 activities initially recorded to 7 broad behavioral categories, based

on contextual similarities. We condensed copulate, incubate, maintain nest, brood, and

provision chick activities to reproductive behavior; preen, bathe, stretch, hop, and shake

activities to self-maintenance behavior; fly and walk activities to locomotion behavior;

forage and drink activities to forage behavior; and sit and rest activities to rest behavior.

Vigilance and alarm activities were not merged. We treated out-of-sight activity category as

missing data. We removed these data from the data set before further analysis.

We pooled data from subject birds into pairs and we defined response variables as

the proportion of time the subject pair was engaged in each of the 7 behavioral categories

during the observation period. We defined human and intraspecific activity predictor

variables as the proportion of time present during each observation. We defined presence of

each human activity type based on the results of the disturbance experiment. To categorize

pedestrian activity, we pooled the 3 pedestrian disturbance treatments and calculated a mean for each nest. We calculated the mean of the nest means, as well as a 95% confidence interval. We used the upper limit of the 95% confidence interval (137 m) to categorize pedestrian activities. We defined human activity as: ped-near – any pedestrian ≤ 137 m of the subject bird; ped-far – any pedestrian 137–300 m from the subject bird; vehicular – any vehicle ≤300 m of the subject bird; and boat – any boat ≤300 m of the subject bird. We defined intraspecific activity as any extra-pair American Oystercatcher ≤ 300 m of the subject bird. We included tide as a categorical predictor variable, defined as 4 3-hr periods during low, mid-rising, high, mid-falling tides. We also included the age of nest for incubation and the age of chicks for brood rearing.

We defined the experimental unit as the nest attempt, for which we made repeated observations. Because repeated observations were unbalanced between attempts and correlations between observations were not constant, we used a mixed-model regression analysis of repeated measures, using the MIXED procedure (SAS Institute Inc 1999). This approach used the maximum likelihood method to estimate parameters and their standard errors and allowed for selection of an appropriate covariance structure that adequately accounted for within-subjects correlation (correlation between repeated measurements on the same nest attempt). We used procedures outlined in Wolfinger (1993) and Littell et al. (2000) to compare candidate models of the repeated measures covariance matrix.

We rarely observed all 7 behavioral categories during a single observation, which resulted in a preponderance of zeros in the data set. No transformation successfully normalized the data; however, the arcsine transformation approached normality. The preponderance of zeros likely had minimal effect on parameter estimates, but may have

inflated standard errors, thus reducing power of the test statistic. To test this possibility, we cross-validated parameter estimates by using log odds transformed data. Estimates were consistent between transformations, so we proceeded with the analysis with the assumption of normality violated. We accepted statistical significance at $\alpha < 0.05$.

We modeled the effects of predictor variables on the response variables, as

$$\arcsin(\sqrt{p_{ij}}) = b_o + b_1 x_{ij1} + b_2 x_{ij2} \ldots b_p x_{ijp} + \varepsilon_{ij}, \quad i = 1, 2, \ldots, 7$$

where p_{ij} was the proportion of time engaged in the ith behavioral category during the jth observation period, b_p was the pth human and intraspecific activity, tide and temperature effects on the ith behavior during the jth observation period, and ε_{ij} was random error associated with the ith activity on the jth observation period.

We considered using a single analysis for each behavioral category to model parameter effects on behaviors, but we abandoned this approach because of the complexity of analyzing all effects within a single model. We used separate models for each reproductive stage (incubation and brood rearing). Further, we hypothesized that response to human activities may change as chicks aged. To test this hypothesis, we included interactions between age and all activity types for the brood-rearing model.

For the disturbance experiment, we defined the nest attempt as the experimental unit, to which we applied disturbance and distance treatments. Because the number of subjects per treatment was unbalanced, we used a simple regression analysis utilizing the method of least squares to fit a general linear model (GLM procedure, SAS Institute Inc1999).

RESULTS

During the 2003 and 2004 breeding seasons, we found 32 nest attempts (19 on the south and 13 on the north end of CINS). We collected 654 hr of observations on 30 of 32 nest attempts (387 hr during incubation and 267 hr during brood rearing). The number of observation hours per nest attempt was dependent on survival of the nest. Mean observations per nest attempt during incubation was 13 and ranged from 1 to 36. Eleven of 32 reproductive attempts successfully produced chicks. We collected observations on all nest attempts during brood rearing. Mean number of observation hours per nest attempt during brood rearing was 24 and ranged from 10 to 38.

During incubation, pairs predominantly engaged in reproductive behavior (Figure 4.1). All other behaviors, such as foraging, resting, and alarm were infrequent. During brood rearing, pairs devoted less time to reproductive behavior and more to all other behaviors, except alarm. Locomotion and vigilance behaviors occurred most frequently during brood rearing, while alarm decreased.

Pairs tended to devote more time to reproductive behavior during high tide during incubation and brood rearing (Figure 4.2). Locomotion and foraging behaviors were frequent at mid-falling and low tides. During brood rearing, pairs devoted more time to self-maintenance, vigilance, and resting behaviors during high tides, although vigilance was consistently high, except during mid-falling tide.

Temperature averaged 27.8° C and 29.8° C for incubation and brood rearing, respectively (Tables 4.1). During incubation, temperature had minor influence on behavior (Table 4.2). Reproductive behavior increased with temperature during brood rearing (Table 4.3).

Mean recorded incubation time was 29.1 d. During incubation, locomotion decreased as nest age increased, but only slightly (Table 4.2). During brood rearing, reproductive behavior decreased as the chicks aged, while self-maintenance, resting, and vigilance behaviors increased (Table 4.3).

Intraspecific activity was the rarest form of disturbance during incubation and brood rearing (Table 4.1), but occurred most frequently to nests on the north end of CINS (Figure 4.4). Reproductive behavior decreased in the presence of intraspecific activity during incubation, and vigilance and alarm increased. During brood rearing, alarm behavior increased in the presence of intraspecific activity.

HUMAN ACTIVITY

Mean proportion of time present of all human activities was 0.14 ($n = 32$, 95% CI = 0.08–0.20). During incubation, ped-near activity was the most common (Table 4.1). Ped-near, ped-far, and boat activities were the most frequent forms of activities during brood rearing (Table 4.1).

Spatial distribution of human activities was variable (Figure 4.3). Mean proportion of time present of all human activities ranged 0–0.67, by nest attempt. Ped-near activity increased for nests in close proximity to points of beach access and the southern tip of CINS. Most ped-far activity occurred on the southern half of the island. Pedestrian activity rarely occurred on the north end. Vehicular activity was distributed across the island, but occurred more frequently on the south end. Boat activity was greater on the north end.

During incubation, oystercatchers in the presence of ped-near activity devoted less time to reproductive behavior and more time to vigilance, locomotion, and alarm

56

behaviors (Table 4.2). Presence of par-far activity had no effect on behavior. In the presence of vehicular activity, pairs devoted more time to reproductive behavior. Vigilance and self-maintenance behavior occurred less frequently. Boat activity had no effect on behavior during incubation.

During brood rearing, ped-near activity had no effect on behavior (Table 4.3). Ped-far activity increased reproductive behavior during brood rearing, although this effect decreased as the chicks aged. In the presence of vehicular activity, alarm behavior increased, but the effect decreased as chicks aged. Oystercatchers devoted less time to foraging behavior during vehicular activity, the effect of which became more pronounced as the chicks aged. Boat activity had no effect on behavior during brood rearing.

We conducted disturbance experiments on 11 pairs during the 2004 season, but because of nest locations and nest failure, we were unable to apply treatments to all nests (Table 4.4). Oystercatcher displacement occurred during all trials of the 20-m pedestrian disturbance treatment. During 40- and 60-m disturbances, displacement occurred during 78% of trials. No vehicle disturbances resulted in displacement and only 1 pair displaced from ATV disturbance. We found no differences among displacement distances ($F_{2, 98} = 0.67$, $P = 0.5157$; Table 4.4). For use in the behavioral analysis, the mean of the pooled nest means for 3 pedestrian disturbance treatments was 113.2 m ($n = 11$, CI = 89.9–136.5 m).

DISCUSSION

Our study provided a time activity budget for American Oystercatchers at CINS during the 2003 and 2004 breeding seasons and illustrated the effects environmental and

anthropogenic factors on American Oystercatcher behavior. Our data suggested that tide, temperature, and intraspecific and human activity influenced oystercatcher behavior.

Our data included activities observable on the breeding territory, or about 71% of the pairs' time budget. Because pairs foraged predominantly away from the breeding grounds, time devoted to foraging may have been low in the overall budget and other behaviors may have been inflated (see Nol 1985). Oystercatcher pairs on CINS devoted most time to reproductive behavior during incubation. In Virginia, females and males incubated 57% and 39% of the time, respectively ($n = 50$, Nol 1985). Time allocated to self-maintenance, locomotion, vigilance, and alarm behaviors during incubation was similar, as was time allocated to vigilance, alarm behaviors during brood rearing, when compared to Nol (1985). Time budgeted to reproduction decreased during brood rearing compared to incubation, and more time was devoted to foraging and vigilance behavior (this study and Nol 1985).

Pairs devoted more time to foraging and locomotion behaviors during mid-falling and low tides during incubation. Oystercatchers feed on marine bivalves, mollusks, worms and other marine invertebrates that inhabit coastal intertidal areas (Bent 1929, Tomkins 1947, Cadman 1980, Johnsgard 1981, J. B. Sabine, personal observation), which are more easily consumed when partially submerged and open during falling and low tides (Nol and Humphrey 1994). If foraging is optimal during mid-falling and low tides, then the corresponding reduction in reproductive behavior may be a concession for the ability to forage efficiently.

During brood rearing, pairs devoted more time to self-maintenance, vigilance, and resting behaviors during mid-rising tide. Energy expenditure by both adults is high

during the breeding season and time for recuperative behavior is limited because of the needs of young (Nol 1985, Verhulst et al. 2001). Recuperative behaviors (self-maintenance and resting) may be more prevalent during this tidal period, because mid-rising tide offers less efficient foraging opportunities.

Temperature and age had little influence on behavior during incubation; however, during brood rearing, reproductive behavior increased with temperature. Reproductive behavior also decreased as the chicks aged. During high temperatures, chicks may need more protection from thermal stress, requiring adults to devote more time to brooding the chicks. Chicks are most vulnerable to thermal stress shortly after hatching, so reproductive activity would be greater earlier in brood rearing (e.g., Dawson and Evans 1960).

Although presence of intraspecific activity was less frequent (0.012 and 0.008 for incubation and brood rearing, respectively) than human activities (0.14), it influenced behavior. Oystercatchers actively defend territories against extra-pair oystercatchers (Kilham 1980, Nol 1985, Nol and Humphrey 1994). At CINS, territorial disputes often consisted of extended chases (>2 min), loud piping displays, and physical contact (stabbing) and involved as many as 4 pairs of oystercatchers. Extra-pair oystercatchers occasionally attacked chicks on CINS (J. B. Sabine, personal observation).

HUMAN ACTIVITY

Most pedestrians were day tourists who accessed the island by ferry and walked across the island to the beach. Because tourists used 2 beach access trails close to the ferry docks, pedestrian activities on the beach concentrated near these crossings. We attributed greater levels of human activity on the south end of CINS to visitors who

accessed the beach by private boat. Occurrence of pedestrian activity decreased quickly with distance from points of beach access. Human activities in other areas of the beach were limited to NPS employees, island residents, and long-distance hikers.

Ped-near activity was greatest during incubation, but decreased during brood rearing. This seems counterintuitive because brood rearing (Jun-Jul) occurred concurrently with the peak tourist season, but there is a logical explanation. Chicks are precocial and are quite mobile within 24–48 h of hatching. Mobile chicks release the family group from the nest site, and enable them to move away from disturbed areas. Because frequency of pedestrian activity decreased with distance from points of beach access, oystercatcher family groups moved as few as 100–200 m from the nest to be a tolerable distance from human activity. This response to human activity was supported by an increase in ped-far activity during brood rearing.

Upon approach by pedestrians, incubating birds discreetly walked off the nest, and stood 10–20 m away, or quickly flew to the surf to mock forage. If the pedestrians continued to approach the nest, the adults responded by calling, flying, and walking quickly near the pedestrians, in an effort to deter the threat. Once the pedestrians passed, the adults briefly resumed vigilance behavior (1–2 min) then returned to the nest. Eurasian Oystercatchers also devote less time to incubation when disturbed on foraging grounds (Verhulst et al. 2001). Although not found in this study, reduced nest attendance may result in delayed fetal development and higher predation rates (Vleck and Vleck 1996, Verhulst et al. 2001).

Incubating oystercatchers did not alter behavior in the presence of ped-far activity, suggesting that the effect of the activity on behavior was negatively correlated

with distance. Biologists have documented a negative correlation between distance of pedestrian disturbance, frequency of disturbance, and reproductive success for other waterbirds as well (Hunt 1972, Burger 1981, Burger and Gochfield 1998, Verhulst et al. 2001, Rodgers and Schwikert 2003).

During incubation, increased reproductive behavior, and decreased self-maintenance and vigilance behaviors suggested that during vehicular activity, the birds' defensive strategy was to avoid attention-drawing behavior. Vehicular activity did not negatively impact reproductive behavior during incubation, suggesting little effect on hatching success. During brood rearing, foraging behavior decreased in the presence of vehicles. Eurasian Oystercatchers allocated fewer food resources to chicks when disturbed while foraging (Verhulst et al. 2001). Hence, reduced foraging of American Oystercatchers due to vehicular activity during brood rearing may have negative impacts on chick survival and ultimately population productivity.

Colonial waterbirds in Florida were less sensitive to boats than pedestrians (Rodgers and Smith 1995). Hence, Rodgers and Smith (1995) recommended no boat zones of 60 to 90 m for colonial waterbirds. Terns in Florida were sensitive to motorboats and personal watercraft (Burger 1998). In contrast, we found that presence of boat activity had no effect on oystercatcher behavior.

We attributed human activity to <10% of reproductive failures (Sabine et al. 2005). One nest failure was directly human induced; a small child walking in the fore dunes destroyed a nest with eggs. One nest that was abandoned was located in an area of frequent pedestrian activity on the south end of the island. Pedestrians searching for shells in the fore dunes frequently caused the incubating bird to flush. For this pair, ped-

near activity was common (0.18). Examination of the eggs after abandonment indicated they contained partially developed embryos. These embryos may have died of thermal stress caused by repeated flushing of the incubating bird induced by human activity.

Nocturnal nest predation by mammals was the primary cause of failure during incubation. Human activity was minimal at night (J. B. Sabine, personal observation). We found no evidence that diurnal nest predation events were related to human activity; therefore our data did not support the hypothesis that disturbance increases parental activity, which increases predation rate (Skutch 1949). Biologists have repeatedly tested this hypothesis without definitive conclusions (Martin 1992, Roper and Goldstein 1997, Martin et al. 2000, Verboven et al. 2001, Tewksbury et al. 2002).

Results of our disturbance experiment were similar to those of Vos et al. (1985), Klein (1993), and Rodgers and Smith (1995) who found greater sensitivity to pedestrian than vehicle activity during incubation. Our results indicated that vehicular activity affected pairs differently during reproductive stages. Other studies also demonstrated variation in the flush distance within and among species of waterbirds in response to human activities (Anderson 1988; Erwin 1989; Rodgers and Smith 1995, 1997; Burger 1998; Rodgers and Schwikert 2002, 2003). Our data supported this variation, with displacement distances from pedestrian disturbance ranging from 27–319 m. Although highly variable, the mean displacement distance between pedestrian disturbance treatments was fairly constant and consistent with no disturbance zone recommendations for similar species. Rogers and Smith (1995) recommended no pedestrian disturbance zones of 178 m for black skimmer (*Rynochops niger*) colonies and 154 m for least tern

colonies. Least Terns flushed at distances of 142–130 m when pedestrians directly approached colonies in Virginia (Erwin 1989).

MANAGEMENT IMPLICATIONS

Differences in behavioral responses between ped-near and ped-far activities during incubation indicated that impacts of disturbance are negatively correlated with distance. Our data indicate that 137 m was a good approximation of American Oystercatchers' threshold of tolerance to human activity during incubation at CINS. Managers at CINS should consider this distance when establishing no disturbance zones. Behavioral responses to ped-near and ped-far activity during brood rearing were mixed, but suggest that the threshold distance increased during brood rearing; hence disturbance free zones of 150 m or greater may be appropriate during brood rearing. When establishing disturbance free zones, managers should also educate pedestrians about the presence of nesting oystercatchers in the area and should encourage pedestrians to move past nesting areas quickly.

Although presence of vehicular activity altered behavior during incubation, reproductive behavior was not impacted negatively, suggesting that vehicular activity at CINS did not affect hatching success. During brood rearing, foraging behavior was lower in the presence of vehicular activity, which may alter chick provisioning and ultimately chick survival. We recommend prohibition of beach driving in oystercatcher territories when chicks are present (late May to late Jul) at CINS.

ACKNOWLEDGMENTS

63

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Table 4.1. Mean presence (proportion) of human and intraspecific activities, and mean temperature (C) during 1-hr observations of American Oystercatcher behavior during incubation and brood rearing, Cumberland Island National Seashore, Georgia, 2003–2004 ($n = 385$ for incubation, $n = 267$ for brood rearing).

Parameter	Mean	SE	Lower 95% CI	Upper 95% CI	Median
Incubation					
Ped-near[a]	0.055	0.009	0.037	0.072	0.000
Ped-far[b]	0.039	0.006	0.027	0.051	0.000
Vehicle[c]	0.015	0.004	0.007	0.022	0.000
Boat[d]	0.024	0.006	0.013	0.035	0.000
Intraspecific[e]	0.012	0.004	0.004	0.020	0.000
Temperature	27.754	0.198	27.367	28.141	27.764
Brood rearing					
Ped-near	0.034	0.008	0.019	0.049	0.000
Ped-far	0.043	0.010	0.024	0.062	0.000
Vehicle	0.021	0.006	0.009	0.033	0.000
Boat	0.037	0.010	0.017	0.056	0.000
Intraspecific	0.008	0.003	0.003	0.013	0.000
Temperature	29.846	0.189	29.475	30.217	29.742

[a] pedestrian ≤137 m of subject bird
[b] pedestrian 138–300 m from subject bird
[c] car, truck, or all-terrain vehicle ≤300 m of subject bird
[d] boat ≤300 m of subject bird
[e] extra-pair American Oystercatcher ≤300 m of subject bird

Table 4.2. Incubation: Parameter estimates of human and intraspecific activity, temperature, and age effects on behavior of American Oystercatchers, Cumberland Island National Seashore, Georgia, 2003–2004.

Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P	Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P
Reproductive behavior						Resting behavior					
Ped-near[a]	**-0.439**	**0.101**	**-0.637**	**-0.240**	**<0.001**	Ped-near	0.067	0.051	-0.032	0.167	0.185
Ped-far[b]	-0.081	0.127	-0.330	0.168	0.523	Ped-far	-0.100	0.063	-0.224	0.024	0.114
Vehicle[c]	**0.471**	**0.203**	**0.071**	**0.870**	**0.021**	Vehicle	-0.086	0.102	-0.286	0.114	0.397
Boat[d]	-0.132	0.147	-0.422	0.157	0.369	Boat	0.056	0.074	-0.089	0.201	0.450
Intraspecific[e]	**-0.725**	**0.237**	**-1.191**	**-0.259**	**0.002**	Intraspecific	-0.156	0.117	-0.387	0.075	0.184
Temperature	0.005	0.004	-0.004	0.013	0.270	Temperature	-0.004	0.002	-0.008	0.000	0.056
Age	0.003	0.002	-0.001	0.006	0.136	Age	0.000	0.001	-0.002	0.002	0.870
Self-maintenance behavior						Vigilance behavior					
Ped-near	-0.037	0.062	-0.159	0.085	0.551	Ped-near	**0.187**	**0.061**	**0.066**	**0.307**	**0.003**
Ped-far	0.032	0.079	-0.124	0.188	0.689	Ped-far	0.029	0.077	-0.123	0.180	0.710
Vehicle	**-0.257**	**0.125**	**-0.504**	**-0.010**	**0.041**	Vehicle	**-0.322**	**0.124**	**-0.565**	**-0.079**	**0.010**
Boat	0.037	0.089	-0.213	0.138	0.674	Boat	0.071	0.089	-0.104	0.246	0.427
Intraspecific	0.084	0.150	-0.211	0.378	0.576	Intraspecific	**0.308**	**0.144**	**0.025**	**0.591**	**0.033**
Temperature	-0.001	0.002	-0.006	0.004	0.643	Temperature	0.002	0.003	-0.003	0.007	0.536
Age	0.001	0.001	-0.001	0.003	0.243	Age	-0.002	0.001	-0.004	0.000	0.110
Foraging behavior						Locomotion behavior					
Ped-near	0.073	0.044	-0.014	0.160	0.099	Ped-near	**0.202**	**0.057**	**0.091**	**0.313**	**<0.001**
Ped-far	-0.020	0.053	-0.124	0.085	0.714	Ped-far	0.121	0.073	-0.023	0.264	0.099
Vehicle	-0.107	0.088	-0.280	0.066	0.225	Vehicle	-0.210	0.115	-0.436	0.016	0.068
Boat	0.059	0.064	-0.066	0.185	0.354	Boat	0.041	0.082	-0.120	0.202	0.613
Intraspecific	0.122	0.096	-0.068	0.312	0.208	Intraspecific	0.260	0.139	-0.013	0.532	0.062
Temperature	0.001	0.002	-0.003	0.004	0.650	Temperature	-0.002	0.002	-0.007	0.002	0.306
Age	-0.001	0.001	-0.003	0.000	0.161	Age	**-0.002**	**0.001**	**-0.004**	**0.000**	**0.018**

Table 4.2. Continued.

Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P	Covariance		
Alarm behavior						Covariance		
Ped-near	**0.091**	**0.037**	**0.018**	**0.163**	**0.014**	Model	Ar(1)[f]	Residual
Ped-far	0.040	0.047	-0.051	0.132	0.387	Reproductive	0.3345	0.0848
Vehicle	0.144	0.074	-0.003	0.290	0.054	Self-maintenance	0.1299	0.0320
Boat	0.061	0.053	-0.044	0.166	0.254	Forage	0.5115	0.0164
Intraspecific	**0.944**	**0.088**	**0.771**	**1.117**	**≤0.001**	Alarm	0.2428	0.0113
Temperature	-0.001	0.001	-0.004	0.002	0.464	Resting	0.3742	0.0213
Age	0.000	0.001	-0.001	0.002	0.446	Vigilance	0.3168	0.0314
						Locomotion	0.0267	0.0267

[a] pedestrian ≤137 m of subject bird
[b] pedestrian 138–300 m from subject bird
[c] car, truck, or all-terrain vehicle ≤300 m of subject bird
[d] boat ≤300 m of subject bird
[e] extra-pair American Oystercatcher ≤300 m of subject bird
[f] first order autoregressive correlation coefficient

Table 4.3.Brood rearing: Parameter estimates of human and intraspecific activity, temperature, and age effects on behavior of American Oystercatchers, Cumberland Island National Seashore, Georgia, 2003–2004.

Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P	Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P
Reproductive behavior						Resting behavior					
Ped-near[a]	0.187	0.265	-0.334	0.708	0.480	Ped-near	-0.169	0.304	-0.767	0.429	0.578
Ped-far[b]	**0.973**	**0.268**	**0.444**	**1.502**	**≤0.001**	Ped-far	-0.472	0.307	-1.078	0.134	0.126
Vehicle[c]	-0.532	0.633	-1.778	0.714	0.404	Vehicle	-0.066	0.726	-1.496	1.364	0.928
Boat[d]	-0.408	0.308	-1.018	0.203	0.189	Boat	0.015	0.353	-0.684	0.713	0.967
Intraspecific[e]	0.285	0.342	-0.389	0.958	0.406	Intraspecific	-0.364	0.393	-1.137	0.409	0.354
Temperature	**0.012**	**0.005**	**0.002**	**0.022**	**0.024**	Temperature	-0.009	0.006	-0.020	0.003	0.145
Age[f]	**-0.015**	**0.002**	**-0.018**	**-0.012**	**≤0.001**	Age	**0.005**	**0.002**	**0.001**	**0.008**	**0.008**
Age*Ped-near	-0.012	0.015	-0.041	0.016	0.398	Age*Ped-near	-0.010	0.017	-0.043	0.023	0.556
Age*Ped-far	**-0.050**	**0.015**	**-0.079**	**-0.021**	**0.001**	Age*Ped-far	0.038	0.017	0.005	0.071	0.026
Age*Vehicle	0.022	0.026	-0.030	0.073	0.403	Age*Vehicle	-0.011	0.030	-0.070	0.048	0.720
Age*Boat	**0.022**	**0.010**	**0.002**	**0.041**	**0.029**	Age*Boat	-0.004	0.011	-0.026	0.018	0.713
Self-maintenance behavior						Vigilance behavior					
Ped-near	0.335	0.198	-0.056	0.726	0.092	Ped-near	-0.181	0.205	-0.585	0.222	0.377
Ped-far	-0.036	0.204	-0.439	0.368	0.862	Ped-far	-0.293	0.212	-0.711	0.126	0.170
Vehicle	0.012	0.476	-0.924	0.949	0.979	Vehicle	0.957	0.490	-0.008	1.922	0.052
Boat	0.037	0.238	-0.434	0.508	0.876	Boat	0.175	0.249	-0.317	0.668	0.483
Intraspecific	-0.035	0.253	-0.533	0.464	0.891	Intraspecific	0.393	0.257	-0.112	0.899	0.127
Temperature	-0.003	0.004	-0.011	0.004	0.385	Temperature	0.002	0.004	-0.006	0.010	0.608
Age	**0.004**	**0.001**	**0.002**	**0.007**	**≤0.001**	Age	**0.005**	**0.001**	**0.002**	**0.007**	**≤0.001**
Age*Ped-near	**-0.022**	**0.011**	**-0.043**	**0.000**	**0.047**	Age*Ped-near	0.018	0.011	-0.004	0.040	0.109
Age*Ped-far	0.001	0.011	-0.021	0.023	0.915	Age*Ped-far	0.014	0.012	-0.009	0.037	0.235
Age*Vehicle	-0.001	0.020	-0.044	0.033	0.781	Age*Vehicle	-0.026	0.020	-0.066	0.014	0.190
Age*Boat	-0.002	0.008	-0.017	0.013	0.755	Age*Boat	-0.007	0.008	-0.022	0.009	0.411

Table 4.3. Continued.

Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P	Parameter	Slope estimate	SE	Lower 95% CI	Upper 95% CI	P
Foraging behavior						Locomotion behavior					
Ped-near	0.044	0.197	-0.344	0.433	0.823	Ped-near	0.150	0.182	-0.208	0.507	0.411
Ped-far	-0.208	0.205	-0.613	0.196	0.311	Ped-far	-0.164	0.184	-0.528	0.200	0.375
Vehicle	**-0.991**	**0.471**	**-1.917**	**-0.064**	**0.036**	Vehicle	0.049	0.436	-0.809	0.907	0.910
Boat	0.375	0.243	-0.106	0.855	0.125	Boat	0.203	0.211	-0.216	0.621	0.340
Intraspecific	0.014	0.243	-0.465	0.493	0.954	Intraspecific	-0.346	0.237	-0.813	0.120	0.145
Temperature	0.001	0.004	-0.006	0.009	0.718	Temperature	-0.002	0.003	-0.008	0.005	0.665
Age	0.000	0.001	-0.003	0.002	0.795	Age	0.001	0.001	-0.001	0.003	0.478
Age*Ped-near	-0.001	0.011	-0.022	0.021	0.962	Age*Ped-near	0.003	0.010	-0.017	0.023	0.767
Age*Ped-far	0.001	0.011	-0.021	0.023	0.919	Age*Ped-far	-0.002	0.010	-0.022	0.018	0.849
Age*Vehicle	**0.042**	**0.019**	**0.004**	**0.080**	**0.033**	Age*Vehicle	0.002	0.018	-0.034	0.037	0.920
Age*Boat	-0.011	0.008	-0.026	0.005	0.168	Age*Boat	-0.009	0.007	-0.023	0.004	0.165
Alarm behavior											
Ped-near	0.039	0.079	-0.118	0.195	0.627	Covariance					
Ped-far	0.054	0.077	-0.098	0.206	0.482	Model	Ar(1)[g]			Residual	
Vehicle	**0.672**	**0.188**	**0.302**	**1.042**	**≤0.001**	Reproductive	0.2240			0.0541	
Boat	-0.018	0.086	-0.188	0.152	0.836	Self-maintenance	0.3153			0.0303	
Intraspecific	**0.719**	**0.104**	**0.514**	**0.924**	**≤0.001**	Forage	0.4133			0.0300	
Temperature	-0.001	0.001	-0.004	0.002	0.627	Alarm	0.0050			0.0050	
Age	0.001	0.000	0.000	0.001	0.237	Resting	0.2153			0.0714	
Age*Ped-near	0.000	0.004	-0.009	0.008	0.974	Vigilance	0.3654			0.0324	
Age*Ped-far	-0.007	0.00	-0.015	0.002	0.121	Locomotion	0.2113			0.0255	
Age*Vehicle	**-0.027**	**0.008**	**-0.042**	**-0.011**	**≤0.001**						
Age*Boat	0.003	0.003	-0.002	0.009	0.219						

[a] pedestrian ≤137 m of subject bird
[b] pedestrian 138–300 m from subject bird
[c] car, truck, or all-terrain vehicle ≤300 m of subject bird
[d] boat ≤300 m of subject bird
[e] extra-pair American Oystercatcher ≤300 m of subject bird
[f] days since hatching

[g] first order autoregressive correlation coefficient

Table 4.4. Mean displacement (Displace) rate and distance (m) for disturbance experiments of 11 pairs of American Oystercatchers, Cumberland Island National Seashore, Georgia, 2004.

Treatment	n	Proportion of Displace	Mean Displace Distance	SE	Lower 95% CI	Upper 95% CI
Ped 20[a]	11	1.00	113.8	18.07	78.4	149.3
Ped 40[b]	10	0.78	118.3	9.36	99.9	136.6
Ped 60[c]	9	0.78	126.4	16.28	94.4	158.3
Vehicle[d]	9	0.00	NA	NA	NA	NA
ATV[e]	8	0.13	169.5	NA	NA	NA

[a] observer walked by nest at 20-m tangential distance
[b] observer walked by nest at 40-m tangential distance
[c] observer walked by nest at 60-m tangential distance
[d] observer drove by nest in a truck at high tide line (approx. 50 m)
[e] observer drove by nest on an all-terrain vehicle at high tide line (approx. 50m)
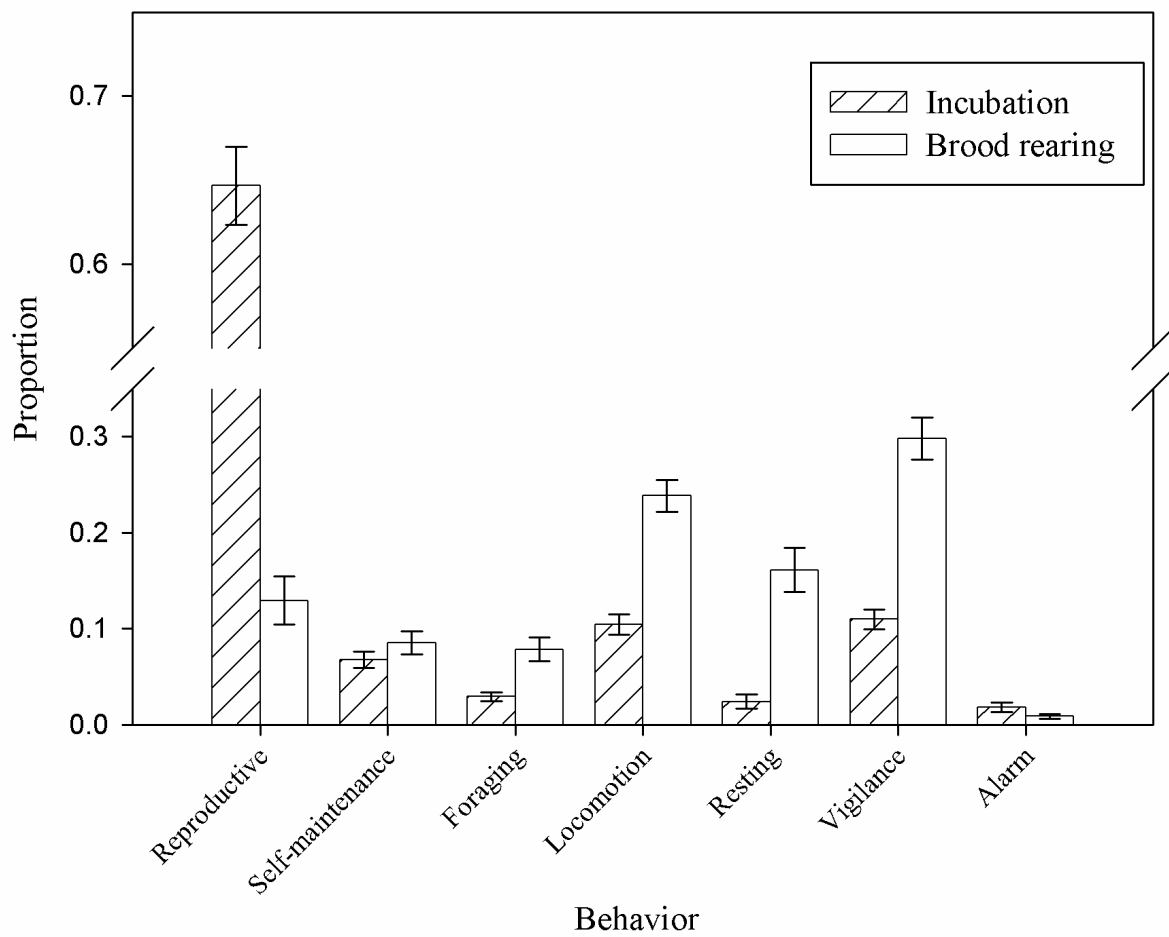
Figure 4.1. Time activity budgets of American Oystercatchers (*Haematopus palliatus)* during brood rearing and incubation at Cumberland Island National Seashore, Georgia, 2003–2004.
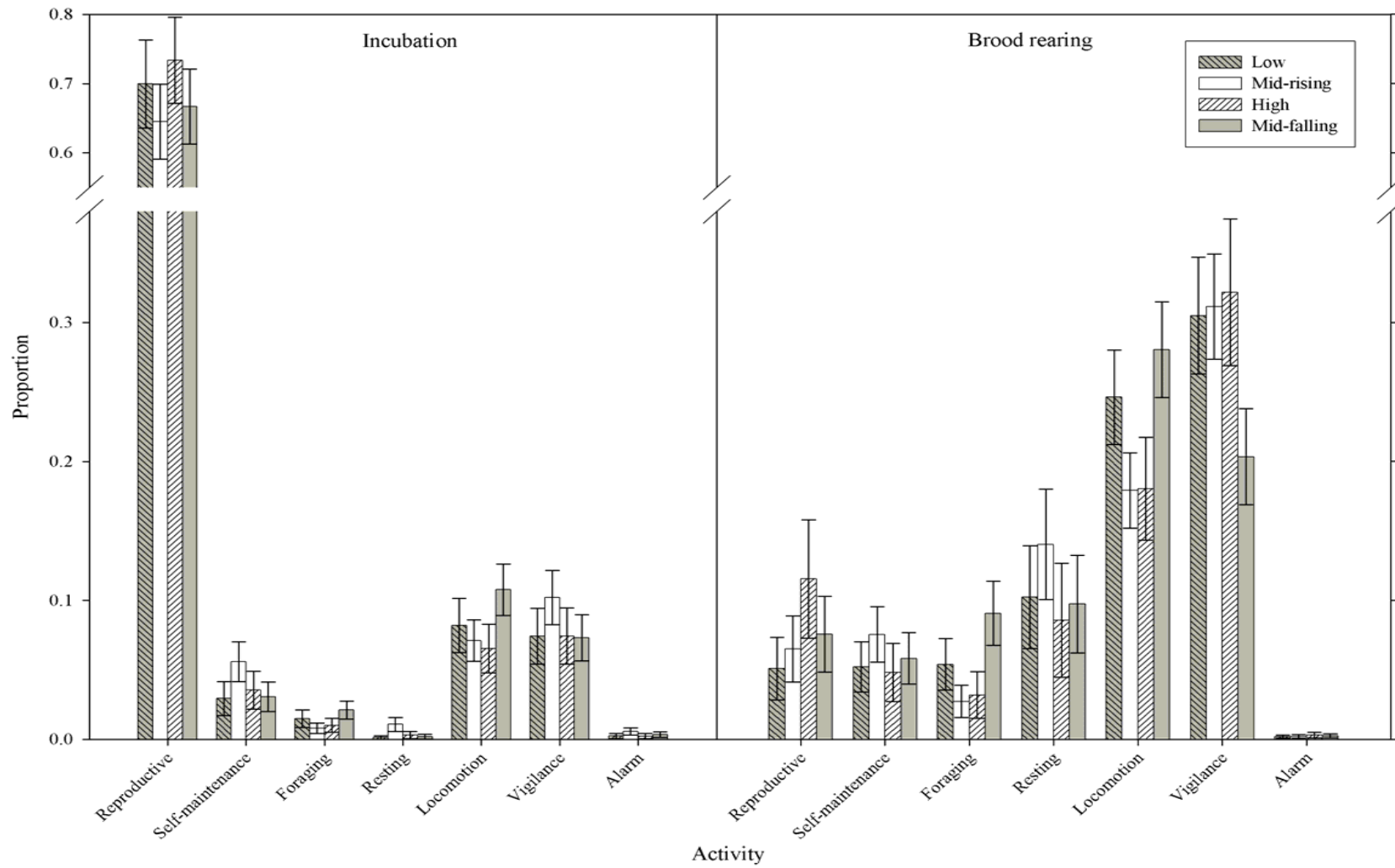
Figure 4.2. Time activity budget by 4 tidal categories of American Oystercatchers (*Haematopus palliatus)* during incubation and brood rearing at Cumberland Island National Seashore, Georgia, 2003–2004.
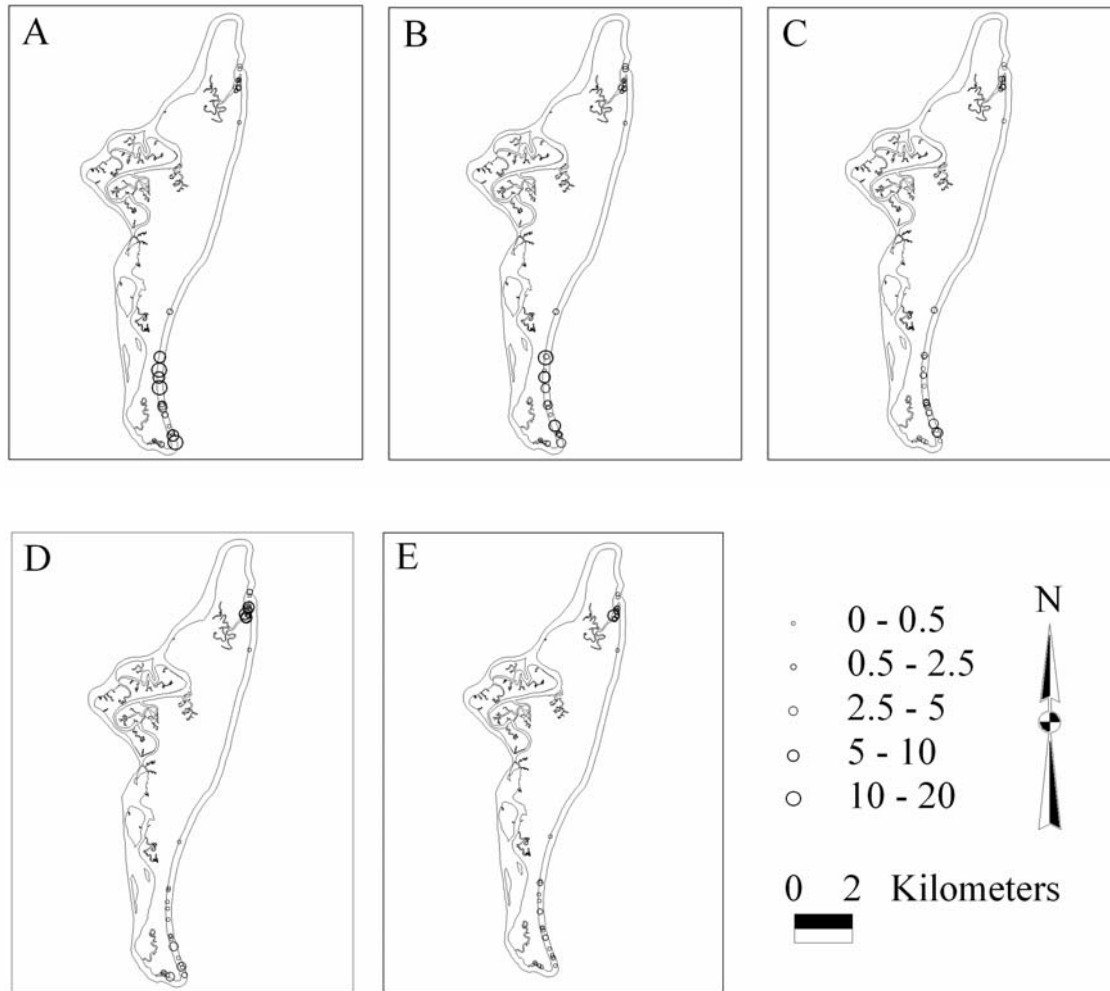
Figure 4.3. Locations of American Oystercatcher (*Haematopus palliatus)* nests at Cumberland Island National Seashore, Georgia, 2003–2004. The size of open circles represents the proportion of time disturbance was present for 5 disturbance types (A) ped-near activity – pedestrian ≤137 m, (B) ped-far activity – pedestrian 138–300 m, (C) vehicle – vehicle ≤300 m of subject bird, (D) boat – boat ≤300 m of subject bird, (E) intraspecific – intraspecific activity ≤300 of subject bird.

CHAPTER 5

CONCLUSIONS

During the 2003 and 2004 breeding seasons, Cumberland Island National Seashore (CINS) supported 11 pairs of American Oystercatchers (*Haematopus palliatus*), which were more reproductively successful than populations documented in other regions of the eastern U.S. Mammalian predation was the primary threat to reproductive success. Human activity around nests affected oystercatcher behavior.

REPRODUCTIVE SUCCESS AND PRODUCTIVITY

Eleven pairs of American Oystercatchers made 32 nest attempts during two seasons (2003 and 2004) at CINS. Nine pairs were successful, fledging 15 chicks. Hatching (32%, 2003; 46%, 2004, apparent nest success) and fledging (21%, 2003; 38%, 2004) success at CINS was higher than previously documented in Georgia and other regions of the eastern U.S. (Nol 1989, Corbat 1990, Toland 1999, Davis et al. 2001, George 2002).

Daily survival was greater on the North End (0.990, 95% CI = 0.982–0.998), than on the South End (0.965, 95% CI = 0.948–0.981) of CINS ($\chi_1^2 = 7.211$, $P = 0.007$). Oystercatchers exhibited spatial variability in daily egg survival on barrier island beaches of North Carolina ranging from 0.9281 ($n = 517$) to 0.9720 ($n = 113$) and on marsh oyster shell rakes and small barrier island beaches in Georgia (George 2002, McGowan et al. 2005). Variability in reproductive success among local populations of oystercatchers appears to be common, and may indicate that local factors strongly influence reproductive success, even within a single island setting. It is unclear how current reproductive rates are affecting population trends, although high annual survival rates of adults and long life spans (17 years, Nol and Humphrey 1994) may

help to sustain populations with low and variable reproduction (Davis 1999). Occasional spikes in reproductive success may be sufficient to sustain or even increase the population (Davis 1999); however, historical records indicate that the population south of Virginia is declining (Davis et al. 2001).

<div align="center">THREATS TO REPRODUCTIVE SUCCESS</div>

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

Predation was the primary cause of nest failure at CINS, accounting for 13 losses during the egg stage and one chick loss over two seasons (7 unknown chick losses). Egg predators were raccoon (*Procyon lotor*, $n = 9$), bobcat (*Lynx rufus*, $n = 3$), and American Crow (*Corvus brachyrhynchos, n = 1*). A ghost crab (*Ocypode quadrata*) preyed on a chick, just after hatching. Except for one predation by a crow, all nests were preyed on at night. Other causes of nest failure included overwash by high tides ($n = 1$), trampling by horses ($n = 1$), abandonment ($n = 2$), and destruction by a child ($n = 1$).

Mammalian predation was the primary cause of nest failure at CINS and it influenced reproductive success between North and South Ends. All predations on the South End were by mammals. Raccoons were the primary nest predator and bobcats, restored to CINS in 1988 (Baker et al. 2001) were a previously undocumented nest predator. At Cape Lookout National Seashore (NS), North Carolina, predation was the cause of 77% of nest failures and raccoons were the primary mammalian predator identified, based on interpretation of signs at the nest site (Davis et al. 2001). There was a negative correlation between predator communities and reproductive success at Cape Lookout NS (McGowan 2004).

Environmental and anthropogenic differences between the north and south ends of CINS may have affected predation rates and causes of nest failure. Human presence may have

maintained higher mammalian predator populations on the south end of CINS (e.g., trash, food). Raccoon and bobcat signs were more prevalent in areas of human activity. In North Carolina, raccoon sightings and signs were more frequent in areas of increased human activity as well (Novick 1996, Davis et al. 2001). Distance from forest to nesting sites (1–2 km) on the north end of CINS may have restricted nest access to mammalian predators. Predations on the north end of CINS were by species that are commonly found on the beach (ghost crab, American Crow) regardless of proximity to forested habitat.

Overwash rarely caused nest failure at CINS in 2003 and 2004. Previously documented in Georgia, flooding was a primary contributor to nest failure (Georgia 2002), although it occurred primarily on sandbars and marshes. Overwash on barrier islands beaches was infrequent (14 of 69, George 2002). Biologists documented flooding as the primary cause of nest failure on low elevation sand spits or marsh habitats in other regions as well (Kilham 1979, Nol 1989, Corbat 1990). The abundance of high elevation nesting habitat in the well-developed dune system at CINS provided ample nesting habitat out of reach of high tides.

Nest failure caused by horse trampling was previously unknown. I frequently observed horses and their tracks and manure on the beach and near nests, suggesting that trampling is a regular source of nest failure from year to year. As much as 23.5% ($n = 17$) of nest failures on Little St. Simons Island resulted from trampling by cattle (Corbat 1990). Feral horses, found on several barrier islands along the East Coast, can also be detrimental to the sensitive dune complex. They graze on vegetation that forms and supports dunes and they trample dunes, resulting in destabilization and erosion of the dune complex (Johnson et al. 1974). Activities of horses potentially destroy nests of several species of ground nesting birds.

Chick loss was a major source of reproductive failure at CINS, but I only documented one loss by camera. Gulls and extra-pair oystercatchers may be chick predators. I observed gulls and other oystercatchers attacking and stabbing chicks without observing mortality; however, a Laughing Gull (*Larus atricilla*) killed an oystercatcher chick in North Carolina (McGowan 2004).

HUMAN ACTIVITY

Generally, human activity at CINS was infrequent (all types present ≤14% of observations), and spatial variation of activity was high (0–40%). Most pedestrians on the beach were day tourists who accessed the island by ferry and walked across the island to the beach. Tourists used two beach access trails in close proximity to the ferry docks and concentrated near these points of access (Dungeness and Sea Camp). I attribute human activity on the southern tip of CINS (south of the jetty) to visitors who accessed the beach by private boat. Occurrence of pedestrian activity decreased as distance from points of access increased. Because the north end of the island was designated as wilderness, disturbance on the north end was limited to NPS employees, island residents, and long-distance hikers. My data support previous studies that have documented variability in human activity levels (Lambeck et al. 1996, Novick 1996, Davis 1999, George 2002).

I documented that American Oystercatchers altered their behavior in the presence pedestrians. During incubation, in the presence of ped-near activity (pedestrian ≤ 137 m of subject pair), pairs devoted less time to reproductive behavior and more time to vigilance, locomotion and alarm behaviors. Upon approach by pedestrians, incubating birds discreetly walked off the nest, and stood 10–20 m away, or quickly flew down to the surf to mock forage. If the pedestrian continued to approach, the adults responded by calling, flying, and walking

quickly in the vicinity of the disturbance, in an effort to deter the threat. Once the pedestrian passed, the adults briefly resumed vigilance behavior (1–2 min) then returned to the nest. We witnessed this behavioral response to approaching pedestrians many times. We rarely observed the passing pedestrians taking notice of the birds. If pedestrians did notice behavior, it usually induced investigation, which resulted in greater disturbance to the birds, further reducing nest attendance. Eurasian Oystercatchers (*H. ostralegus*) disturbed on foraging grounds, spend more time foraging and less time incubating (Verhulst et al. 2001). Although not documented by this study, reduced nest attendance may result in delayed fetal development and higher predation rates (Vleck and Vleck 1996, Verboven et al. 2001).

During incubation, pairs did not alter behavior in the presence of ped-far activity (pedestrian 138–300 m of subject pair), suggesting that the effect of disturbance by pedestrians on behavior was negatively correlated with distance. This behavioral response of beach-nesting and wading birds to disturbance by humans and subsequent negative effects on reproductive success has been confirmed by other studies along the Atlantic Coast (Hunt 1972, Burger 1981, Burger and Gochfield 1998, Verhulst et al. 2001, Rodgers and Schwikert 2003).

Vehicular activities (vehicle ≤300 m of subject pair) were short (≤1 min), but affected oystercatcher behavior. During incubation, reproductive behavior increased and self-maintenance and vigilance behaviors decreased during vehicular activity, suggesting that the defensive strategy was to avoid detection. Alarm and locomotion responses to the approach of vehicles were different from responses to disturbance by pedestrians; however, I have no explanation for these effects. Vehicular activity did not negatively impact reproductive behavior during incubation, suggesting little effect on hatching success.

I documented that boat activity (boats ≤300 m of subject pair) had no effect on behavior during incubation or brood rearing. This is in contrast to previous studies that documented sensitivity to boats. In Florida, colonial waterbirds were less sensitive to boats than to pedestrians (Rodgers and Smith 1995). Hence, Rodgers and Smith (1995) recommended no boat zones of 60–90 m for colonial waterbirds. Terns were sensitive to motorboats and personal watercraft in Florida (Burger 1998). I may not have detected changes in behavior because my definition of boat disturbance was too broad. By reducing my definition to boats within 100 m or less, I may have found differences in behavioral response.

Ped-near activity was most frequent during incubation, but decreased during brood rearing. Mobile chicks freed the family group from the nest site, enabling them to move away from areas of human activity. Because frequency of pedestrian activity decreased as distance from points of beach access increased, family groups may have moved as few as 100–200 m to be a tolerable distance from human disturbance. This response to human activity was supported by the increase in frequency of ped-far activity during brood rearing.

I found no behavioral response to ped-near activity during brood rearing. This is difficult to explain, particularly because results indicate that presence of ped-far activity altered reproductive behavior. Contrary to my results, I suspect that oystercatcher behavior is altered in the presence of ped-near activity. Perhaps responses to ped-near activity varied between pairs to such a degree that results lacked clear significance in any direction, or this study lacked the sample size necessary to detect behavioral changes.

Ped-far activity did alter reproductive behavior during brood rearing, suggesting that pairs are more sensitive to pedestrian activity at greater distances. Eurasian oystercatchers allocated fewer resources to chicks when disturbed by humans on foraging grounds (Verhulst et

al. 2001). Reduced foraging activity during brood rearing in response to human activity may have impacts on chick survival and ultimately population productivity.

Results from the disturbance experiment indicated that oystercatchers were more sensitive to pedestrian disturbance than vehicle disturbance during incubation, but these findings are not novel because others have documented this response (Vos et al. 1985, Klein 1993, Rodgers and Smith 1995). The mean flush distances among pedestrian disturbance treatments were not different ($F_{2, 98} = 0.55$, P = 0.5157) and similar to no pedestrian zone recommendations for other beach nesting species. No pedestrian zone distances of 178 m for Black Skimmer (*Rynochops niger*) colonies and 154 m for Least Tern (*Sterna antillarum*) colonies in Florida have been recommended (Rodgers and Smith 1995). In Virginia, Least Terns flushed at distances of 142 to 130 m when biologist approached colonies directly (Erwin 1989).

Disturbance from human activities caused <10% of reproductive failures (*n* = 23 failures relative to 32 total nests, based on video recordings of nest failures). Humans caused one nest failure directly – a child (approx. 3 y/o) walking in the fore dunes, found a nest, and destroyed the eggs. One abandoned nest was located in an area of frequent human activity on the south end of CINS. Pedestrians searching for shells in the fore dunes frequently caused the incubating bird to temporarily abandon the nest. Ped-near activity was present 18% of the time, greater than the island mean (6%). The adults abandoned the nest after 35 days of incubation. I examined the eggs several days after abandonment and found partially developed embryos. Although research indicates that American Oystercatcher eggs are tolerant of temperature extremes (Nol and Humphrey 1994), these embryos may have died of thermal stress or inconsistent incubation temperature caused by human induced, repeated temporary abandonment of the nest by the incubating bird.

Nocturnal nest predation by mammalian predators was the primary cause of failure during incubation, when direct human disturbance was minimal. I found no evidence that diurnal nest predation events (e.g., trampling by horses, tidal overwash, etc.) were related to activities of humans, so our data does not support the hypothesis that disturbance at the nest site increases parental activity, thus attracting nest predators and decreasing reproductive success (Skutch 1949). Biologists have repeatedly tested this hypothesis without definitive conclusions (Martin 1992, Roper and Goldstein 1997, Martin et al. 2000, Verboven et al. 2001, Tewksbury et al. 2002).

MANAGEMENT RECOMMENDATIONS

At CINS, predation of eggs by mammals was the primary cause of nest failure and was greater on the south end. Cursory observations of bobcat and raccoon tracks and scat on the beach suggested that use of the beach by these animals may have been greater on the south end. Activities of humans (especially litter and deposition of trash in open dumpsters) on the south end may be attracting and supporting larger populations of predators. The ability to use the beach at CINS for recreational purposes is probably one of the primary reasons people visit the island, so completely restricting beach use by tourists is not a viable management option; however, covering trash cans and sealing dumpsters from raccoons and other scavengers may be a simple way to reduce mammalian predators. Visitors accessing CINS by a personal boat without paying the park entrance fee is against NPS regulations (J. Fry, personal communication) and may exceed CINS daily visitor quotas. Access by this means is especially prevalent on the south end, where disturbance to nesting American Oystercatchers, Wilson's Plovers and Least Terns is common. I recommend that NPS staff at CINS monitor south end use by boaters, and restrict access as per NPS regulation.

Predator control is a proven technique for increasing reproductive success of American Oystercatchers (McGowan 2004) and may be an effective, although temporary, means of increasing reproductive success of American Oystercatchers on the south end of CINS. This management tool is labor intensive, long-term, and often very expensive. Additionally, in areas of frequent human activity, predator control can be difficult to implement safely; however, as demonstrated by the recent feral hog reduction campaign, the staff at CINS have proven their ability to implement predator control safely and effectively. Priority should be placed on raccoon population reduction on the beach. Staff are already removing small numbers of raccoons from the beach because of predation of loggerhead sea turtle eggs, so implementing a more intensive removal program may be possible. Staff could use procedures already in place for raccoon and feral hog control (i.e., trapping).

The north end of CINS is an area of high reproductive success for American Oystercatchers, compared to other nesting areas along the Atlantic coast. Human activity on the north end is low and nesting sites are protected from predators by distance from forested habitat, both of which benefit reproductive success. Currently the north end of CINS is protected from most human activity under the Wilderness Act of 1964. Greater use of the north end for recreation purposes would attract predators and disrupt nesting activities, so efforts should be made to maintain the area's Wilderness status and minimize tourist activity.

Trampling of nests by horses was an uncommon source of nest failure during the 2003 and 2004 breeding seasons; however, horse activity on the beach suggests that this may be a regular source of nest failure from year to year, perhaps greater than documented by this study. Feral horses use the beach to escape insects and the heat of the island interior. They graze dune-forming vegetation and trample dunes, resulting in destabilization and erosion of the dune

complex (Johnson et al. 1974) and potentially destroy nests of several species of ground-nesting birds. These horses are destructive and harmful to the ecosystem of the island, so their numbers should be reduced significantly and they should be excluded from sensitive areas.

Although disturbance by human activity at CINS was relatively infrequent, disturbance was frequent enough to detect behavioral changes by oystercatchers in response to human activity. Measures should be taken to minimize disturbance to reproductively active pairs. On the south end, human activity was frequent and directly attributed to nest failure. I caution against using the results of this study for areas other than CINS, because patterns of human activity and the responses of oystercatchers may be different in other areas; however, in areas of frequent human disturbance, greater behavioral alteration and nest failure may be expected.

Differences in behavioral response between ped-near and ped-far activities during incubation indicate that impacts of disturbance are negatively correlated with distance and suggest that 137 m is a good approximation of American Oystercatchers' threshold of tolerance disturbance at CINS. Typically managers erect signs that warn pedestrians of nesting birds, which are connected by a light string, termed "symbolic fencing" (Erwin et al. 2002). These signs are currently being used at CINS to warn pedestrians of Least Tern colonies. I recommend posting signs in a radius $\geq$ 137 m around active American Oystercatcher nests.

Behavioral responses to ped-near and ped-far activities during brood rearing were mixed, but suggest that the threshold of tolerance to disturbance increases during brood rearing. Signs posted $\geq$ 150 m from pairs with chicks may be appropriate during brood rearing. Following hatching, signs posted during incubation could be moved to the recommended distance. Some pairs, especially those on the north end, may move chicks away from the nest site shortly after

hatching. Family groups should be monitored in the days following hatching and signs should be repositioned if the family groups relocate.

Staff at CINS should educate tourists about the presence of nesting oystercatchers during the breeding season, how to identify nests and nesting behavior, and encourage pedestrians to quickly move through nesting areas they encounter. This could be added to the orientation seminar that is given to all visitors upon arrival.

Although presence of vehicular activity altered behavior during incubation, reproductive behavior was not negatively impacted, suggesting that vehicular activity at CINS in 2003 and 2004 did not negatively impact hatching success. During brood rearing, foraging behavior was lower in the presence of vehicular activity, which may alter chick provisioning and ultimately chick survival. To minimize impacts on adult foraging behavior, I recommend the prohibition of beach driving in oystercatcher territories (within 150 m) when chicks are present. At all other times, beach driving should be limited to well below the high tide line and speeds should be limited to 10 mph or less, so drivers have ample time to see and react to birds in the path of travel.

RECOMMENDATIONS FOR FUTURE RESEARCH

- To further our knowledge of threats to American Oystercatcher reproductive success, identification of the causes of nest failure using video monitoring equipment should be expanded to include all nesting habitats.
- Further research is needed to monitor annual American Oystercatcher reproduction at important areas and to identify other areas of high reproductive success, so these areas can be protected from human and predator encroachment.

- Radio telemetry would allow biologists to follow chicks very closely and locate chick remains following mortality, although identification of the cause of death may still be difficult.

- Further research is needed to investigate how greater frequency of human activity than found at CINS affects behavior and reproductive success.

- Effects of human activity on reproductive success and behavior in other habitats should be studied as well. Human activity on foraging grounds may reduce food intake or chick provisioning which may lead to reduced survival of chicks and adults. Eurasian Oystercatchers allocate fewer resources to chicks when adults were disturbed on foraging grounds (Verhulst et al. 2001). Pairs that nest in other habitats may be subjected to different forms and levels of human activity than those nesting on oceanfront beaches, which may affect behavior and reproductive success as well.

- Sea turtle management is common throughout beaches on the southern Atlantic coast. These management programs involve extensive beach driving, often at night. My data indicated that vehicular activity did affect behavior during incubation and brood rearing, and may reduce fledging success. It is unknown how vehicular activity at night affects behavior and reproductive success. These effects should be examined further.

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APPENDIX A: American Oystercatcher clutch data from Cumberland Island National Seashore, Georgia, 2003 and 2004.

Nest ID	Location	Latitude	Longitude	Initiation	Clutch Size	Failure	Cause	Hatch Date	Hatched	Fledged	Fledge Date
1	S	30 56 21.9	81 24 16.6	04/05/03	3	04/30/03	Raccoon		0	0	
2	S	30 55 56.5	81 24 22.9	04/05/03	2			05/10/03	2	2	06/14/03
3	S	30 44 18.5	81 27 25.7	04/11/03	3	04/30/03	Unknown		0	0	
4	S	30 43 00.4	81 27 33.9	04/12/03	2	04/17/03	Overwash		0	0	
5	S	30 45 39.7	81 27 35.8	04/16/03	2	04/26/03	Bobcat		0	0	
6	S	30 56 11.9	81 24 17.5	04/04/03	3			05/03/03	1	1	06/07/03
7	S	30 56 01.7	81 24 17.3	04/18/03	2			05/16/03	2	2	06/20/03
8	S	30 43 23.7	81 27 02.6	04/18/03	3	04/28/03	Raccoon		0	0	
9	S	30 56 51.4	81 24 14.8	04/19/03	3			05/21/03	1	1	06/25/03
10	S	30 43 00.3	81 26 53.6	04/30/03	3	05/04/03	Raccoon		0	0	
11	S	30 43 04.0	81 27 44.1	05/01/03	2	06/08/03	Raccoon		0	0	
12	S	30 47 49.5	81 27 08.2	05/12/03	3	05/31/03	Raccoon		0	0	
13	S	30 43 19.5	81 27 00.8	05/12/03	2	05/25/03	Bobcat		0	0	
14	S	30 44 26.3	81 27 27.8	05/12/03	2	05/31/03	Bobcat		0	0	
15	S	30 45 00.7	81 27 33.7	05/12/03	3	06/22/03	Unknown	06/08/03	1	0	
16	N	30 56 19.1	81 24 20.1	05/14/03	2	06/10/03	Ghost Crab	06/09/03	1	0	
17	S	30 44 02.6	81 27 19.9	06/12/03	2	06/23/03	Raccoon		0	0	
18	S	30 43 17.0	81 26 58.9	06/12/03	1	07/17/03	Abandoned		0	0	
19	S	30 46 09.6	81 27 32.5	06/14/03	2	07/15/03	Horse		0	0	
20	S	30 44 23.3	81 27 27.5	04/07/04	3			05/04/04	3	1	06/08/04
21	S	30 45 24.4	81 27 36.0	04/11/04	3			05/10/04	3	2	06/14/04
22	N	30 55 54.9	81 24 24.0	04/11/04	2	05/15/04	Abandoned		0	0	
23	N	30 56 11.0	81 24 17.6	04/11/04	3			05/10/04	2	2	06/14/04
24	N	30 56 17.9	81 24 17.3	04/14/04	3			05/13/04	2	2	06/17/04
25	N	30 54 45.6	81 24 15.2	04/16/04	2	04/24/04	Raccoon		0	0	
26	N	30 56 43.6	81 24 14.9	04/13/04	3			05/13/04	3	2	06/17/04
27	S	30 43 06.5	81 27 46.7	04/22/04	3	05/05/04	Raccoon		0	0	
28	S	30 43 37.1	81 27 09.9	04/21/04	3	06/17/04	Unknown	05/21/04	2	0	
29	S	30 46 04.7	81 27 34.4	04/30/04	2	05/09/04	Human		0	0	
30	N	30 56 00.8	81 24 17.9	05/05/04	3	05/27/04	Crow		0	0	
31	S	30 42 56.5	81 27 29.1	05/17/04	2	06/08/04	Raccoon		0	0	
32	N	30 56 03.0	81 24 26.3	05/30/04	2	07/09/04	Unknown		0	0	

APPENDIX B: Mean presence (%) of human activities near American Oystercatcher nest attempts (± 2 SE) during incubation, Cumberland Island National Seashore, Georgia, 2003 and 2004.

Nest ID	Hours of Observation	Per-near[a] Activity	Ped-far[b] Activity	Vehicular[c] Activity	Boat[d] Activity	Total Activity
02	4	0	1.65	0	17.08	18.73
		(0)	(5.24)	(0)	(54.37)	(52.85)
03	1	6.67	0	1.67	0	8.33
		(0)	(0)	(0)	(0)	(0)
05	1	34.58	0	0	0	34.58
		(0)	(0)	(0)	(0)	(0)
06	1	0	0	0	0	0
		(0)	(0)	(0)	(0)	(0)
07	4	4.91	2.01	0	0	6.91
		(15.63)	(6.39)	(0)	(0)	(22.03)
08	1	3.49	0	0	0	3.49
		(0)	(0)	(0)	(0)	(0)
09	9	0.24	2.42	0.86	2.15	5.67
		(0.55)	(4.67)	(1.86)	(4.62)	(6.42)
10	2	37.27	9.66	0	3.18	50.11
		(16.37)	(42.03)	(0)	(40.38)	(14.72)
11	18	0	0.55	0	1.09	1.63
		(0)	(1.15)	(0)	(1.34)	(1.63)
12	11	3.35	3.37	3.18	0.15	10.06
		(5.16)	(4.50)	(4.46)	(0.33)	(13.00)
13	8	1.35	7.91	11.48	7.81	28.55
		(3.21)	(12.43)	(26.52)	(18.48)	(55.56)
14	12	1.15	1.29	0.98	0	3.43
		(1.72)	(2.10)	(1.71)	(0)	(2.78)
15	17	18.21	4.36	0.35	0.06	22.99
		(13.99)	(4.09)	(0.41)	(0.12)	(14.64)
16	10	0	0.50	1.29	3.63	5.42
		(0)	(1.13)	(2.92)	(7.48)	(8.27)
17	9	2.96	0.53	1.59	3.02	8.09
		(4.72)	(0.85)	(1.86)	(6.62)	(8.57)
18	27	17.75	5.85	7.79	0.67	32.05
		(10.96)	(5.52)	(8.08)	(1.37)	(17.45)
19	19	17.20	1.42	1.23	0	19.85
		(12.44)	(2.51)	(0.86)	(0)	(12.66)
20	24	8.64	11.20	0.42	0	20.27
		(7.94)	(9.21)	(0.50)	(0)	(12.63)
21	20	11.05	16.58	1.70	0	29.32
		(7.32)	(9.33)	(1.91)	(0)	(15.23)
22	28	0	0	0	5.17	5.17
		(0)	(0)	(0)	(4.48)	(4.48)
23	4	0	0	0	0	0
		(0)	(0)	(0)	(0)	(0)
24	26	0.76	0	0.49	4.98	6.24
		(1.26)	(0)	(0.63)	(4.98)	(5.66)

APPENDIX B: Continued.

Nest ID	Hours of Observation	Per-near[a] Activity	Ped-far[b] Activity	Vehicular[c] Activity	Boat[d] Activity	Total Activity
25	5	0.18	0.74	0	0	0.92
		(0.52)	(2.04)	(0)	(0)	(2.56)
26	12	0.12	12.64	0.95	0	13.72
		(0.26)	(19.32)	(2.10)	(0)	(19.38)
27	4	0	0	0	0	0
		(0)	(0)	(0)	(0)	(0)
28	21	0.54	3.28	2.78	0	6.59
		(1.11)	(4.82)	(2.44)	(0)	(5.44)
29	6	40.09	27.04	0.51	0	67.64
		(38.35)	(24.12)	(1.31)	(0)	(39.54)
30	21	0	1.47	0.52	0	2.00
		(0)	(3.08)	(0.66)	(0)	(3.60)
31	26	2.13	1.34	0.32	4.77	8.56
		(2.15)	(1.41)	(0.66)	(6.20)	(6.74)
32	36	0	0	0	10.83	10.83
		(0)	(0)	(0)	(9.51)	(9.51)

[a] pedestrian ≤137 m of subject bird
[b] pedestrian 138–300 m from subject bird
[c] car, truck, or all-terrain vehicle ≤300 m of subject bird
[d] boat ≤300 m of subject bird
[e] extra-pair American Oystercatcher ≤300 m of subject bird

APPENDIX C: Mean presence (%) of human activities near American Oystercatcher nest attempts (± 2 SE) during brood rearing, Cumberland Island National Seashore, Georgia, 2003 and 2004.

Nest ID	Hours of Observation	Per-near[a] Activity	Ped-far[b] Activity	Vehicular[c] Activity	Boat[d] Activity	Total Activity
02	16	0	0	0	8.09	8.09
		(0)	(0)	(0)	(13.23)	(13.23)
06	22	0	0	0	4.02	4.02
		(0)	(0)	(0)	(7.96)	(7.96)
07	26	2.08	0	2.98	2.22	7.28
		(2.93)	(0)	(5.24)	(4.46)	(8.85)
09	20	0	0	0.08	3.66	3.75
		(0)	(0)	(0.18)	(4.94)	(4.92)
15	10	30.15	10.15	1.44	0	41.75
		(17.63)	(16.55)	(2.34)	(0)	(26.16)
20	28	2.90	0.72	2.38	0	6.00
		(5.96)	(0.88)	(1.98)	(0)	(6.77)
21	38	12.17	14.14	2.29	0.22	28.82
		(6.76)	(7.36)	(1.16)	(0.33)	(10.93)
23	27	0	1.73	0.12	9.53	11.38
		(0)	(2.50)	(0.26)	(10.71)	(12.92)
24	23	0	0	0	15.26	15.26
		(0)	(0)	(0)	(14.29)	(14.29)
26	29	0.07	0.18	1.27	0.36	1.87
		(0.13)	(0.36)	(1.92)	(0.37)	(1.95)
28	28	0.57	15.59	10.09	0	26.25
		(0.65)	(13.29)	(10.18)	(0)	(21.78)

[a] pedestrian ≤137 m of subject bird
[b] pedestrian 138–300 m from subject bird
[c] car, truck, or all-terrain vehicle ≤300 m of subject bird
[d] boat ≤300 m of subject bird
[e] extra-pair American Oystercatcher ≤300 m of subject bird

APPENDIX D: Mean time (%) devoted to behaviors by American Oystercatcher pairs (± 2 SE) during incubation, Cumberland Island National Seashore, Georgia, 2003 and 2004.

Nest ID	Reproductive Behavior	Self-maintenance Behavior	Foraging Behavior	Locomotion Behavior	Resting Behavior	Vigilance Behavior	Alarm Behavior
02	67.07	0.21	6.62	15.16	0	9.01	1.92
	(73.49)	(0.68)	(21.08)	(28.69)	(0)	(18.36)	(6.12)
03	70.83	2.50	0	11.67	0	15.00	0
	(0)	(0)	(0)	(0)	(0)	(0)	(0)
05	91.67	0	0	4.58	0	0.83	2.92
	(0)	(0)	(0)	(0)	(0)	(0)	(0)
06	66.67	1.37	5.02	14.16	0	8.68	4.11
	(0)	(0)	(0)	(0)	(0)	(0)	(0)
07	67.86	11.18	0.53	6.55	0	6.63	7.25
	(56.46)	(33.38)	(1.02)	(9.01)	(0)	(17.01)	(22.63)
08	100.00	0	0	0	0	0	0
	(0)	(0)	(0)	(0)	(0)	(0)	(0)
09	78.09	5.14	0	8.31	0.05	7.83	0.58
	(25.42)	(8.45)	(0)	(11.47)	(0.11)	(10.87)	(1.34)
10	49.14	0.63	4.18	20.77	1.27	13.46	10.55
	(167.11)	(7.97)	(53.17)	(150.81)	(10.80)	(20.24)	(54.35)
11	72.34	7.16	1.30	6.71	1.58	10.77	0.14
	(12.99)	(5.01)	(1.35)	(2.82)	(3.25)	(6.29)	(0.29)
12	57.97	5.15	6.57	14.41	4.62	9.57	1.71
	(16.77)	(4.48)	(6.03)	(8.30)	(6.63)	(5.29)	(3.34)
13	85.56	0.56	0.99	8.31	0	2.91	1.67
	(12.46)	(0.77)	(1.85)	(9.29)	(0)	(3.51)	(3.21)
14	72.64	3.27	2.80	11.78	0	9.44	0.07
	(17.44)	(2.70)	(3.29)	(10.80)	(0)	(6.25)	(0.15)
15	56.92	5.49	5.26	16.31	5.42	7.42	3.18
	(14.96)	(4.85)	(4.25)	(7.07)	(9.06)	(4.00)	(4.50)
16	70.34	6.90	0.56	6.40	3.27	11.38	1.15
	(15.13)	(7.14)	(0.50)	(3.12)	(3.18)	(9.10)	(2.09)
17	66.73	11.25	1.02	5.70	0	13.39	1.91
	(26.10)	(10.25)	(1.06)	(3.27)	(0)	(14.33)	(3.08)
18	61.01	4.64	3.63	11.83	3.89	11.71	3.28
	(8.83)	(2.50)	(1.99)	(3.56)	(3.56)	(3.82)	(3.06)

Nest ID	Reproductive Behavior	Self-maintenance Behavior	Foraging Behavior	Locomotion Behavior	Resting Behavior	Vigilance Behavior	Alarm Behavior
19	51.26	5.73	6.64	21.12	3.82	10.26	1.17
	(12.59)	(2.83)	(3.21)	(9.97)	(3.80)	(4.63)	(1.67)
20	59.48	7.65	3.56	14.49	1.36	11.63	1.83
	(7.79)	(4.06)	(1.73)	(4.94)	(1.73)	(3.95)	(1.95)
21	51.17	8.07	4.27	17.13	5.12	14.03	0.21
	(11.28)	(3.46)	(2.32)	(6.32)	(5.06)	(6.24)	(0.25)
22	65.39	7.32	3.70	7.66	2.02	12.06	1.85
	(6.39)	(3.11)	(1.60)	(1.89)	(2.14)	(3.66)	(1.64)
23	73.52	8.92	2.71	7.79	0.85	6.21	0
	(33.73)	(16.78)	(4.98)	(13.05)	(2.70)	(14.72)	(0)
24	67.83	6.36	3.52	8.27	2.29	8.81	2.92
	(8.58)	(3.03)	(1.72)	(2.53)	(2.71)	(3.33)	(2.59)
25	54.17	11.50	4.10	11.37	5.38	12.75	0.74
	(11.76)	(13.33)	(9.25)	(9.26)	(13.39)	(5.18)	(2.04)
26	75.15	6.33	1.72	5.36	4.80	6.64	0
	(10.97)	(3.77)	(1.84)	(3.84)	(5.00)	(3.93)	(0)
27	53.01	11.51	0.81	3.97	14.45	14.54	1.71
	(7.83)	(15.75)	(1.68)	(8.45)	(24.81)	(19.67)	(5.44)
28	63.93	7.65	3.58	9.34	1.37	13.44	0.69
	(8.54)	(3.53)	(3.12)	(2.72)	(1.57)	(5.80)	(0.86)
29	43.22	5.24	3.22	16.33	1.30	26.79	3.91
	(16.45)	(6.00)	(4.63)	(12.22)	(2.75)	(16.66)	(5.22)
30	75.60	3.58	1.55	8.14	1.30	7.60	2.24
	(9.48)	(2.38)	(1.27)	(3.29)	(1.77)	(3.68)	(3.77)
31	68.88	6.60	1.32	7.87	1.45	13.55	0.33
	(8.20)	(3.30)	(0.65)	(2.14)	(1.50)	(4.36)	(0.37)
32	62.12	11.53	1.28	7.23	1.18	13.12	3.54
	(6.48)	(3.83)	(0.63)	(1.66)	(2.00)	(2.86)	(2.27)

APPENDIX E: Mean time (%) devoted to behaviors by American Oystercatcher pairs (± 2 SE) during brood rearing, Cumberland Island National Seashore, Georgia, 2003 and 2004.

Nest ID	Reproductive Behavior	Self-maintenance Behavior	Foraging Behavior	Locomotion Behavior	Resting Behavior	Vigilance Behavior	Alarm Behavior
02	4.08	17.58	10.64	18.65	25.04	22.47	1.55
	(4.93)	(6.57)	(5.26)	(6.40)	(11.90)	(4.57)	(1.58)
06	13.16	21.71	4.19	19.52	10.58	30.23	0.60
	(10.06)	(6.49)	(3.02)	(6.55)	(5.40)	(7.49)	(0.57)
07	6.00	3.86	13.48	29.74	18.14	28.31	0.47
	(3.58)	(2.02)	(5.85)	(5.98)	(7.77)	(6.92)	(0.58)
09	11.52	9.41	5.40	24.14	17.02	31.86	0.65
	(9.48)	(3.97)	(3.10)	(6.05)	(7.85)	(7.00)	(0.56)
15	36.32	8.48	6.52	24.72	6.61	16.51	0.84
	(15.62)	(5.41)	(5.33)	(9.67)	(6.30)	(6.30)	(1.69)
20	4.03	7.97	4.79	25.27	13.42	43.93	0.59
	(2.36)	(3.44)	(3.18)	(6.14)	(6.65)	(8.77)	(0.58)
21	22.30	5.71	5.20	25.09	13.72	27.50	0.48
	(8.42)	(2.09)	(2.50)	(3.98)	(7.39)	(6.32)	(0.35)
23	10.15	9.54	10.73	25.85	11.44	30.58	1.70
	(6.05)	(4.94)	(4.85)	(5.63)	(4.05)	(6.90)	(1.00)
24	4.42	6.80	9.86	22.92	24.77	29.83	1.40
	(4.61)	(2.69)	(4.04)	(5.50)	(9.22)	(6.06)	(0.96)
26	15.22	5.16	12.22	27.92	10.85	27.41	1.21
	(9.51)	(2.11)	(4.26)	(5.36)	(6.56)	(6.42)	(1.08)
28	20.43	4.98	3.78	15.80	25.28	29.26	0.47
	(10.86)	(2.44)	(3.02)	(4.04)	(9.81)	(8.03)	(0.37)