Effects of Human Activity on Behavior of Breeding American Oystercatchers, Cumberland Island National Seashore, Georgia, USA

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Abstract.—Increased human use of coastal areas threatens the United States population of American Oystercatchers (*Haematopus palliatus*), a species of special concern. Biologists often attribute its low numbers and reproductive success to human disturbance, but the mechanism by which human presence reduces reproductive success is not well understood. During the 2003 and 2004 breeding seasons, 32 nesting attempts of American Oystercatchers were studied on Cumberland Island National Seashore (CINS). Behavior was examined with and without human activity in the area to determine how human activity affected behavior. The oystercatchers' behavioral responses (proportion time) were analyzed with and without human or intraspecific disturbances using mixed models regression analysis. Proportions of time human activities were present (≤300 m from oystercatchers) during observations averaged 0.14 (N = 32, 95% CI = 0.08-0.20). During incubation, pedestrian activity near (≤137 m) oystercatchers reduced the frequency of occurrence of reproductive behavior, but pedestrian activity far (138-300 m) from oystercatchers had no effect. Vehicular and boat activities (≤300 m) had minimal effects on behavior during incubation. During brood rearing, an effect of pedestrian activity near oystercatchers was not evident; however, pedestrian activity far from oystercatchers increased the frequency of reproductive behavior. Vehicular and boat activity had no effects on behavior during brood rearing. Of 32 nesting attempts, two failed (<10%) because of human disturbance and were located in areas of greater human activity (south end). Managers on CINS should minimize pedestrian activity near nests (≤137 m) during incubation. During brood rearing, protection from pedestrian activity should be increased, when possible, to >137 m and vehicular activity should be minimized at current levels or less. *Received 02 May 2007, accepted 20 September 2007.*

Key words.—American Oystercatcher, behavior, Cumberland Island, Georgia, *Haematopus palliatus*, human disturbance, reproductive success, shorebird, time activity budgets.

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American Oystercatchers (*Haematopus palliatus*) are coastal marine specialists that nest on barrier island beaches with well-developed dune complexes along the Atlantic Coast of North America (Nol and Humphrey 1994). The American Oystercatcher may be particularly susceptible to human activity because >50% of the United States human population lives in coastal areas (Bookman *et al.* 1999). Although coastal areas in Georgia have remained relatively undeveloped, the human population in coastal Georgia has increased at a rate of 20% each decade (National Oceanographic and Atmospheric Administration 2003). Biologists often have attributed low numbers of oystercatchers and population declines in Georgia, North Carolina, and Florida to increased human presence (Rappole 1981; Below 1996; Toland 1999; McGowan and Simons 2006). American Oystercatcher populations of the Mid-Atlantic states are also declining (Mawhinney and Bennedict 1999; Nol *et al.* 2000; Davis *et al.* 2001) such that the United States Shorebird Conservation Plan lists American Oystercatcher as a species of high priority, with a breeding population estimated at <11,000 individuals (Brown *et al.* 2001, 2005).

The mechanisms by which human activities affect American Oystercatchers are not well understood, but human disturbance reduced Eurasian Oystercatchers' (*H. ostralegus*) fledgling success by reducing foraging time and allocation of prey to chicks (Verhulst *et al.* 2001). Similarly, researchers also documented a negative relationship between human activities and reproductive success of African (*H. moquini*; Jeffery 1987) and Canarian Black Oystercatchers (*H. meadewaldoi*; Hockey 1987; Leseberg *et al.* 2000) in South Africa. Recently, the effects of human recreation on incubation of American Oystercatchers have been also documented in North Carolina (McGowan and Simons 2006).

The probability of nest failure was greater among American Oystercatchers in areas of greater human activity at Cape Lookout National Seashore, North Carolina (Novick 1996; Davis 1999), but the mechanism by which human presence reduced reproductive success was unclear. Oystercatchers left nests for several minutes as vehicles approached. Human induced exposure of eggs when adults are off nests may put eggs at greater risk of predation and thermal stress (Vleck and Vleck 1996; Davis 1999). As established in North Carolina, mammalian predator abundance was higher in areas of human activity, and likely increased the probability of nests being preyed upon (Davis 1999). Increased parental activity caused by human presence attracts predators and increases nest predation rates (Skutch 1949; Martin *et al.* 2000; Tewksbury *et al.* 2002).

To better understand oystercatcher behavior, investigators must account for behavioral changes induced by naturally occurring environmental variations as well as those affected by human disturbance. Environmental factors that influence behavior of American Oystercatchers include tidal cycles, wherein frequency of foraging behavior increases during falling and low tides, and thermal conditions such as high temperatures that stimulate gular flutter (Nol and Humphrey 1994). Intraspecific interactions may elicit intense territorial defense and antagonistic behaviors (Nol 1985). To investigate how human activity affects American Oystercatcher behavior, oystercatchers were studied 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 this concern, a population of American Oystercatchers was studied for which nest fates were known (Sabine *et al.* 2005, 2006).

Study objectives were to: (1) compare breeding behavior of a population of American Oystercatchers during natural environmental fluctuations to oystercatcher behavior in the presence of human activity, (2) estimate a distance threshold of tolerance to human activity, and (3) relate effects of human activity to video documented causes of nest failure. It was suspected that human disturbance would induce behaviors that would reduce reproductive success.

METHODS

Study Area

Investigations were conducted on Cumberland Island National Seashore (CINS), a 14,736-ha barrier island in Georgia (30°N, 81°W). The northern tip (four linear km) and southern portion (eleven linear km) of the island had wide sloping beaches and well-developed dune system that provided nesting habitat for several species, including Least Terns (*Sterna antillarum*), Gull-billed Terns (*S. nilotica*), Wilson's Plovers (*Charadrius wilsonia*), and ten (2003) to twelve (2004) pairs of American Oystercatchers.

Tourists, National Park Service (NPS) employees and volunteers, and island residents traveled on the beach by foot, vehicle, and all-terrain vehicle (ATV). Visitors also accessed the beach by boat. 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 wilderness, was free of most human disturbance, except occasional NPS employees (including diurnal turtle nesting surveys conducted daily; no nocturnal turtle surveys were conducted), tourists with backcountry permits, and residents with beach driving permits (N = 326, C. Gregory, Georgia Dept. Nat. Res., pers. comm.). The NPS recorded 41,612 recreational visits to the island in 2003 and 38,258 in 2004 (NPS, unpubl. data). Many unrecorded visitors gained access to the island by boat, (ten to 15 boats/d) on its southern end (J. B. Sabine, pers. obs.).

Data Collection

Daily surveys were conducted along the beach to locate all American Oystercatchers and nests during 2003 and 2004 (Mar-Aug). Nest locations were recorded using a global positioning system (Garmin GPS 12, Garmin International, Inc., Olathe, KS), were marked with a 30-cm florescent orange stake (paint stirrer placed ca. three m seaward of nest), and number of eggs was recorded. Video monitoring equipment was placed at the nest to record activity and causes of nest failure within 24 h of locating it (Sabine *et al.* 2005).

Within 24 h of locating a nest, observations of the breeding pair were initiated to estimate their activity time budget. Data were collected with the aid of spotting scopes and binoculars from a blind (≥50 m from nest), from a vehicle on the beach (usually 300 m from birds, but less when pairs and hatchlings approached vehicle), or from a boat (300 m from nest). Individuals were not marked, so pairs were assumed to maintain their territories throughout the breeding season.

Each day was divided into four equal time intervals: 06.00-08.59, 09.00-11.59, 12.00-14.59, and 15.00-17.59 h. Because pairs were widely dispersed, it was impossible to collect data on pairs at random, which would also cause more human disturbance on the beach. Therefore, sampling effort was distributed for pairs as evenly as possible among time intervals and reproductive periods. Behavioral data were collected for 30 min for each member of the breeding pair during each one-h observation session. When two observers were used, both birds were observed for 30 min simultaneously; when only one observer was used, birds were observed in random succession. Data were collected on breeding pairs during incubation at the nest until the clutch failed or hatched, and during brood rearing at the nest or in the territory until failure or fledging. Hatchlings were assumed to fledge at age 35 d (Nol and Humphrey 1994).

During each 30-min observation session, instantaneous behavior was recorded at 15-s intervals using a metronome (Wiens *et al.* 1970; Baldassarre *et al.* 1988) for a total of 120 observations per session. Eighteen behaviors were identified [modified from Nol (1985)] based on observations made before initiation of the study: copulate; incubate = sitting or standing directly over nest; maintain nest = placing breast on nest rim and using scraping motion with feet to deepen nest or remove debris; brood = sitting or standing directly over chicks with wings partially extended; provision chick = presenting and breaking food for chicks; preen = using 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 probe 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; and alarm = piping display, head bobbing, chasing, being chased, or other agonistic behavior. If the subject bird was not directly observable, it was recorded as such and assigned no behavior outcome.

Tidal phase was recorded and defined as four 3-h periods (low, mid-rising, high, mid-falling tides). Age of nests or chicks (days since clutch initiation or hatching) and ambient surface temperature were recorded, also. During 2004, surface temperature was recorded from five randomly chosen nesting sites and five random locations within the oystercatchers' typical nesting habitat (backshore and fore dunes). Each temperature data logger was housed in a 15-cm long, 2.54-cm diameter white PVC pipe (schedule 40) and was mounted on a stake vertically five cm above ground surface. Pipes were capped on top and left open on the bottom. Data loggers recorded ambient temperature every five min throughout the breeding season. All sets of temperatures were averaged to obtain a mean surface temperature for the island. Because surface temperature was not recorded in 2003, temperature data were obtained from the nearest weather station (Golden Isles Airport, Brunswick, GA). Linear regression analysis was used to create a predictive equation to estimate mean surface temperature (y) on the island given mean daily temperature recorded at the weather station (x) in 2004: $y = 1.061 + 0.989x$, $r^2 = 0.86$, $P \leq 0.001$. Weather station data for 2003 were used in this equation to obtain estimates of daily ambient temperature on the island for 2003.

Intraspecific interaction regularly disturbed pairs, but occurrence was not uniform in the study area (J. B. Sabine, pers. obs.). Extra-pair oystercatchers were included in the analysis to account for conspecific effects on behavior. Data were not collected on interactions with other species present on the study site because these interactions were rare relative to human and intraspecific interactions.

Data on anthropogenic disturbances were collected in the vicinity (≤300 m) of the pair during each observation session. These data included type of disturbance (pedestrian, vehicle, or boat) and approximate distance of the disturbance from the subject bird. The two closest disturbances were recorded when multiple disturbances were present.

To assess the distance at which various forms of anthropogenic disturbance induced an overt behavioral response by incubating oystercatchers, or a threshold of tolerance, a disturbance experiment was conducted with eleven breeding pairs in 2004. Forms of disturbance were mimicked that typically occurred in the area (vehicular, ATV, and pedestrian traffic) by driving or walking by nests, parallel with the beach. Three distances were used for pedestrian disturbance trials (treatments = 20, 40, and 60 m seaward of the nest). For vehicle and ATV disturbance trials, each nest was driven by immediately below the high tide line (ca. 50 m seaward of nests). During each trial the incidence of displacement from the nest was recorded (incubating bird walked from nest). If displacement occurred, the driver stopped and took the line of sight measurement from the disturbance to the nest using a laser rangefinder. From one to four trials of each disturbance type and distance were conducted at each nest until hatching or nest failure. Trials were limited to once daily per nest during cooler conditions. If the experimental disturbance caused displacement, distance measurements were recorded quickly and observers left the area immediately, allowing the bird to return to the nest.

Potentially human-induced nest failure documented on video (i.e., nest destruction or abandonment) was compared with levels of human activity at the nest site to assess the effects of human disturbance on reproductive success. Research was conducted under a University of Georgia Animal Care and Use Permit (A2002-10207-cl) and NPS Scientific Research and Collecting Permit (CUIS-2003-SCI-0002).

Statistical Analysis

Recorded activities (18) were classified to seven broad behavioral categories, based on contextual similarities. Copulate, incubate, maintain nest, brood, and provision chick activities were condensed to "reproductive" behavior; preen, bathe, stretch, hop, and shake activities to "self-maintenance" behavior; fly and walk activities were condensed to "locomotion" behavior; forage and drink activities were condensed to "forage" behavior; and sit and rest activities were condensed to "rest" behavior. Vigilance and alarm activities were not merged. Out-of-sight observations were treated as missing data and removed before further analysis.

Data from subject birds were pooled by nesting attempt for each of the seven broad behavioral categories that were defined as response variables, i.e., frequency of that behavior, expressed as a proportion of non-missing instantaneous observations (≤120) recorded in each 30-min session on each bird of the pair (total ≤240/60 min). Proportions of time human or intraspecific activities were present were predictor values.

To categorize pedestrian activity, the three treatments for pedestrian disturbance were pooled ($P > 0.05$) from the disturbance experiment and a mean distance was calculated at which adults were displaced from each nest. An average and 95% confidence interval (CI) was calculated from the means for each nest. The upper limit of the CI (95% CL_U) was used as a conservative estimate of oystercatchers' threshold of tolerance. Disturbance data were categorized based on this threshold for pedestrian activities as near (ped-near) or far (ped-far) from the nests or nestlings. Vehicular activities were defined as any boat or vehicle ≤300 m from the subject bird. Intraspecific activity was defined as any extra-pair American Oystercatcher ≤300 m of the subject bird. Tidal phase was included as a categorical predictor variable and age (d) of nests and chicks was added as ordinal predictor variables in the model for incubation and brood rearing stages, respectively.

Experimental unit was defined as nest attempt for which repeated observations were made. Because repeated observations were unbalanced among attempts and correlations between observations were not constant, a mixed-model regression analysis of repeated measures (MIXED procedure, SAS Institute, Inc. 1999) was used. This approach used the maximum likelihood method to estimate parameters and their standard errors and permitted selection of an appropriate covariance structure [selected AR(1) = autoregressive order 1, based on AIC analysis] that adequately accounted for within-subjects correlation (correlation between repeated measurements on the same nest attempt). Procedures outlined in Wolfinger (1993) and Littell *et al.* (2000) were used to compare candidate models of the repeated measures covariance structure.

All seven behavioral categories were rarely observed during a single observation session, resulting in a preponderance of zeros in the data set. No transformation successfully normalized the data; however, distributions of the response proportions were made more symmetric by use of arcsine transformation. The preponderance of zeros likely had minimal effect on parameter estimates, but may have inflated standard errors, thus reducing power of the test statistic.

Effects of predictor variables on the response variables were modeled for each of the seven transformed response variables as $\arcsin(\sqrt{p_{ij}}) = b_o + b_1x_{ij1} + b_2x_{ij2} \ldots b_px_{ijp} + \varepsilon_{ij}$, where p_{ij} was the frequency of occurrence of the behavior during the i^{th} observation session, b_p was the effect of the p^{th} variable (human activity, intraspecific activity, tide and temperature) on the response during the i^{th} observational period, and ε_{ij} was random error associated with the i^{th} observation period.

Consideration was given to analyze each behavioral response in a single model for the entire reproductive period, but the expected relationship between response and the covariates would depend on reproductive stage (incubation and brood rearing). Because interactions associated with reproductive stage would have greatly increased the complexity of the analysis, this approach was abandoned in favor of separate models for incubation and brood rearing stages. Furthermore, the response to human activities was hypothesized to change as chicks aged. To test this hypothesis, interactions between chick age and all human activity types were included for the brood-rearing model.

The accepted level of significance ($\alpha = 0.05$) was corrected to experiment-wide error rate by a Bonferroni adjustment for incubation ($\acute{\alpha} = 0.007$) and brood rearing ($\acute{\alpha} = 0.005$) to account for multiple testing (Sokal and Rohlf 1995).

RESULTS

During the 2003 and 2004 breeding seasons, 32 nest attempts were found (19 on the south and 13 on the north end of CINS) for 21 pairs (Sabine *et al.* 2006 for details). Distribution and densities of oystercatchers' nests were similar between years. Six-hundred fifty-four h of oystercatcher observations were collected on 30 of 32 nest attempts (387 h during incubation and 267 h during brood rearing). The number of observation hours per nest attempt was dependent on survival at the nest. Mean hours observed per nest attempt were 13 and ranged from one-36 h during incubation. Eleven of 32 reproductive attempts successfully produced chicks. Observations were collected on eleven family groups during brood rearing. Mean hours observed were 24 and ranged from ten to 38 h per family group during brood rearing. On average, seven additional hours of observation were out of sight during brood rearing.

During incubation, pairs engaged predominantly in reproductive behavior (Fig. 1). All other behaviors, such as self maintenance, foraging, resting, and alarm were much less frequent. Locomotion and vigilance behaviors were more frequent than self maintenance, foraging, resting, and alarm behaviors, but less frequent than reproductive behaviors during incubation. The reverse of this pattern occurred during brood rearing when reproductive behaviors were recorded less frequently than locomotion and vigilance behaviors. Locomotion or vigilance also occurred more frequently than all other behaviors during brood rearing (Fig. 1).

During incubation and brood rearing, reproductive behavior was similar in all tidal phases (Fig. 1). Locomotion and foraging behaviors were more frequent at mid-falling tides than at mid-rising or high phases dur-

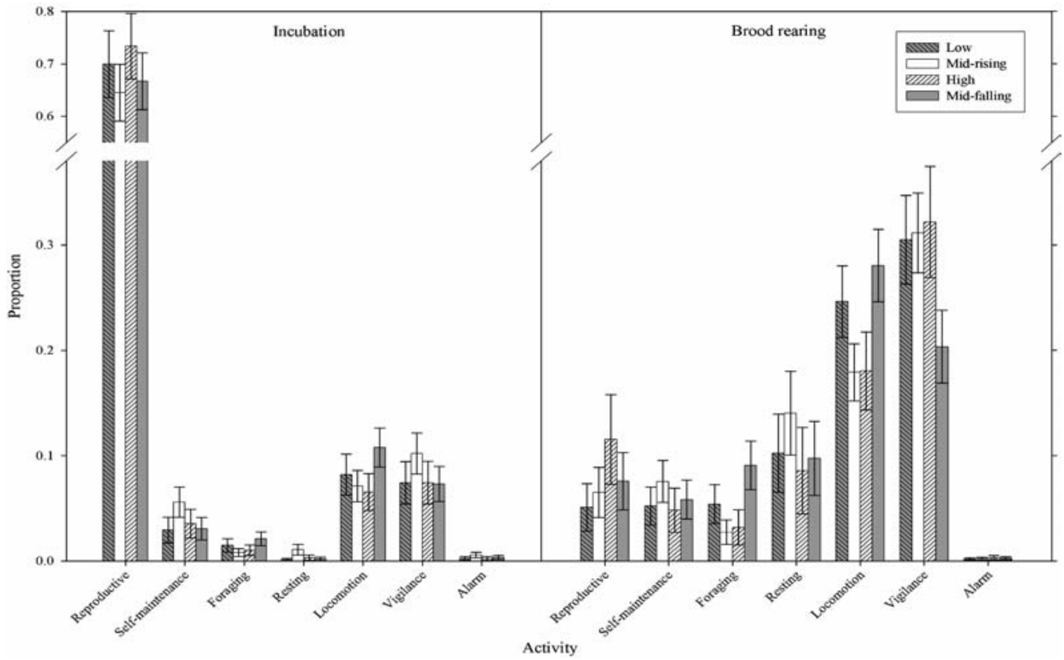

Figure 1. Mean proportions (95% CI) by nesting attempts for American Oystercatcher activity budgets showing effects of four tidal categories during incubation and brood rearing on Cumberland Island National Seashore, Georgia, 2003-2004.

ing incubation and brood rearing. During brood rearing, vigilance behaviors were less frequent at mid falling tides than at any other tidal phase (Fig. 1).

Temperature averaged 27.8°C and 29.8°C during incubation and brood rearing, respectively (Table 1). During incubation and brood rearing, temperature had no effect on behavior (Tables 2 and 3). Mean incubation time was 29.1 d. During brood rearing, frequency of reproductive behavior decreased as the chicks aged, while frequency of self-maintenance and vigilance behaviors increased (Table 3).

Intraspecific activity was the rarest form of disturbance during incubation and brood rearing (Table 1), but it occurred more frequently at nests on the north end of CINS. During brood rearing, frequency of alarm behavior increased in the presence of intraspecific activity (Table 3).

Mean proportion of the 60-min observation time per pair during which at least one human activity was present was 0.14 (n = 32, 95% CI = 0.08-0.20). During incubation, ped-near and ped-far activities were the most common (Table 1). Ped-near, ped-far, and boat activities were the most frequent forms of activities during brood rearing (Table 1).

Spatial distribution of human disturbance activities was variable on CINS (Fig. 2). Mean proportion of observation time during which human activities were present ranged from zero to 0.67, by nest attempt. Ped-near activity increased for nests near points of beach access and the southern tip of CINS. Most ped-far activity occurred on the southern half of the island with little pedestrian activity on the north end (Fig. 2). Vehicular activity was distributed across the island but was also more frequent on the south end. Boat activity was more frequent on the north end because of the proximity of Christmas Creek, a popular fishing location.

During incubation, oystercatchers disturbed by ped-near activity reduced their frequency of reproductive behavior and increased vigilance and locomotion behaviors (Table 2). Upon approach by pedestrians, incubating birds discreetly walked from the nest and stood ten to 20 m away or then flew quickly to the surf to mock forage. If the pe-

Table 1. Mean proportion of observation sessions (one h each) of American Oystercatcher nesting attempts with proximate human or intraspecific activities and mean temperature (C) during incubation and brood rearing, Cumberland Island National Seashore, Georgia, 2003-2004 (N = 387 observation h for incubation, N = 267 observation h for brood rearing).

Predictor variable	Mean	CI_L[a]	CI_U[a]
Incubation			
Ped-near[b]	0.055	0.037	0.072
Ped-far[c]	0.039	0.027	0.051
Vehicle[d]	0.015	0.007	0.022
Boat[e]	0.024	0.013	0.035
Intraspecific[f]	0.012	0.004	0.020
Temperature	27.8	27.4	28.1
Brood rearing			
Ped-near[b]	0.034	0.019	0.049
Ped-far[c]	0.043	0.024	0.062
Vehicle[d]	0.021	0.009	0.033
Boat[e]	0.037	0.017	0.056
Intraspecific[f]	0.008	0.003	0.013
Temperature	29.8	29.5	30.2

[a]95% CI (CI_L = lower, CI_U = upper).
[b]Pedestrian ≤137 m of subject pair.
[c]Pedestrian 138-300 m from subject pair.
[d]Car, truck, or all-terrain vehicle ≤300 m of subject pair.
[d]Boat ≤300 m of subject pair.
[f]Extra-pair American Oystercatcher ≤300 m of subject pair.

destrians 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 and then returned to incubate (one to two min). Presence of ped-far activity had no overt effect on behavior during incubation (Table 2). In the presence of vehicles during incubation, oystercatchers modified reproductive behavior, vigilance, and self-maintenance behavior (Table 2), but none of these behaviors were significantly changed from periods with no vehicles within 300 m. Boat activity had no effect on behavior during incubation (Table 2).

During brood rearing, oystercatchers did not modify any of their behaviors with ped-near activity (Table 3). Ped-far activity caused an increased frequency of reproductive behavior during brood rearing, but this effect decreased as chicks aged (Age*Ped-far interaction, Table 3). In the presence of vehicular activity, frequency of alarm behavior increased, but the effect decreased as chicks aged (Age*Vehicle interaction, Table 3). Oystercatchers may have exhibited foraging behavior less frequently when vehicular activity occurred, but not significantly. Boat activity had no overt effect on behaviors during brood rearing.

Disturbance experiments were conducted on eleven oystercatcher pairs during the 2004 season, but because of nest locations and nest failure, all treatments could not be applied to all nests (Table 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. The mean distance for displacement of pooled nest means (all three treatments) was 113 m (N = 11, 95% CI = 90-137 m). No vehicle disturbance trials resulted in displacement from nests and only one pair displaced from an ATV disturbance trial. The upper value of the 95% CI (137 m) was used as a conservative threshold of tolerance of nesting American Oystercatchers on CINS.

Human activity caused two reproductive failures. A child caused one failure directly on the south end when he walked into the foredunes, handled two eggs, dropped them, and destroyed the nest. For the second pair, also on the south end, chronic disturbances occurred

Table 2. Estimated effects of human and intraspecific activity, temperature, and nest age (d) predictor variables on frequency of occurrence of American Oystercatcher behavior during incubation, Cumberland Island National Seashore, Georgia, 2003-2004. P-values <0.007 are considered significant for experimentwise error rate (P ≤ 0.05) after Bonferroni adjustment.

Predictor variable	Slope estimate	CI_L[a]	CI_U[a]	P	Predictor variable	Slope estimate	CI_L[a]	CI_U[a]	P
Reproductive behavior					Resting behavior				
Ped-near[b]	-0.439	-0.637	-0.240	<0.001	Ped-near	0.067	-0.032	0.167	n.s.
Ped-far[c]	-0.081	-0.330	0.168	n.s.	Ped-far	-0.100	-0.224	0.024	n.s.
Vehicle[d]	0.471	0.071	0.870	n.s.	Vehicle	-0.086	-0.286	0.114	n.s.
Boat[e]	-0.132	-0.422	0.157	n.s.	Boat	0.056	-0.089	0.201	n.s.
Intraspecific[f]	-0.725	-1.191	-0.259	n.s.	Intraspecific	-0.156	-0.387	0.075	n.s.
Temperature	0.005	-0.004	0.013	n.s.	Temperature	-0.004	-0.008	0.000	n.s.
Age	0.003	-0.001	0.006	n.s.	Age	0.000	-0.002	0.002	n.s.
Self-maintenance behavior					Vigilance behavior				
Ped-near	-0.037	-0.159	0.085	n.s.	Ped-near	0.187	0.066	0.307	<0.005
Ped-far	0.032	-0.124	0.188	n.s.	Ped-far	0.029	-0.123	0.180	n.s.
Vehicle	-0.257	-0.504	-0.010	n.s.	Vehicle	-0.322	-0.565	-0.079	n.s.
Boat	0.037	-0.213	0.138	n.s.	Boat	0.071	-0.104	0.246	n.s.
Intraspecific	0.084	-0.211	0.378	n.s.	Intraspecific	0.308	0.025	0.591	n.s.
Temperature	-0.001	-0.006	0.004	n.s.	Temperature	0.002	-0.003	0.007	n.s.
Age	0.001	-0.001	0.003	n.s.	Age	-0.002	-0.004	0.000	n.s.
Foraging behavior					Locomotion behavior				
Ped-near	0.073	-0.014	0.160	n.s.	Ped-near	0.202	0.091	0.313	<0.001
Ped-far	-0.020	-0.124	0.085	n.s.	Ped-far	0.121	-0.023	0.264	n.s.
Vehicle	-0.107	-0.280	0.066	n.s.	Vehicle	-0.210	-0.436	0.016	n.s.
Boat	0.059	-0.066	0.185	n.s.	Boat	0.041	-0.120	0.202	n.s.
Intraspecific	0.122	-0.068	0.312	n.s.	Intraspecific	0.260	-0.013	0.532	n.s.
Temperature	0.001	-0.003	0.004	n.s.	Temperature	-0.002	-0.007	0.002	n.s.
Age	-0.001	-0.003	0.000	n.s.	Age	-0.002	-0.004	0.000	n.s.
Alarm behavior					Alarm behavior				
Ped-near	0.091	0.018	0.163	n.s.	Intraspecific	0.944	0.771	1.117	≤0.001
Ped-far	0.040	-0.051	0.132	n.s.	Temperature	-0.001	-0.004	0.002	n.s.
Vehicle	0.144	-0.003	0.290	n.s.	Age	0.000	-0.001	0.002	n.s.
Boat	0.061	-0.044	0.166	n.s.					

[a]95% CI (CI_L = lower, CI_U = upper).
[b]Pedestrian ≤137 m of subject pair.
[c]Pedestrian 138-300 m from subject pair.
[d]Car, truck, or all-terrain vehicle ≤300 m of subject pair.
[e]Boat ≤300 m of subject pair.
[f]Extra-pair American Oystercatcher ≤300 m of subject pair.

(ped-near = 18% frequency) and probably caused failure indirectly. Pedestrians, searching for shells in the foredunes, frequently caused this pair to leave their nest. Their eggs, examined after abandonment, contained partially developed embryos, perhaps killed by thermal stress caused by repeated flushing of the incubating birds. Indirect effects of human activity, i.e., open trash containers (with raccoons observed feeding) and human food or fish bait left on beaches (J. Sabine and J. Meyers, pers. obs.), may be associated with large numbers of mammalian predators, mainly raccoons, on the south end. This end of CINS, which not only had a lower nest success than the north end (Sabine *et al.* 2006), also had much higher disturbances (five to ten times the frequency) from pedestrians (Fig. 2).

DISCUSSION

This study provided information on the frequency of occurrence of behaviors relative to different disturbances of American Oyster-

Table 3. Estimated effects of human and intraspecific activity, temperature, and age of chicks (days) predictor variables on frequency of occurrence of American Oystercatcher behavior during brood rearing behavior, Cumberland Island National Seashore, Georgia, 2003-2004. P-values <0.005 are considered significant for experimentwise error rate (P ≤ 0.05) after Bonferroni adjustment.

Parameter	Slope estimate	CI_L[a]	CI_U[a]	P	Parameter	Slope estimate	CI_L[a]	CI_U[a]	P
Reproductive behavior					Resting behavior				
Ped-near[b]	0.187	-0.334	0.708	n.s.	Ped-near	-0.169	-0.767	0.429	n.s.
Ped-far[c]	0.973	0.444	1.502	≤0.001	Ped-far	-0.472	-1.078	0.134	n.s.
Vehicle[d]	-0.532	-1.778	0.714	n.s.	Vehicle	-0.066	-1.496	1.364	n.s.
Boat[e]	-0.408	-1.018	0.203	n.s.	Boat	0.015	-0.684	0.713	n.s.
Intraspecific[f]	0.285	-0.389	0.958	n.s.	Intraspecific	-0.364	-1.137	0.409	n.s.
Temperature	0.012	0.002	0.022	n.s.	Temperature	-0.009	-0.020	0.003	n.s.
Age[g]	-0.015	-0.018	-0.012	≤0.001	Age	0.005	0.001	0.008	n.s.
Age*Ped-near	-0.012	0.016	0.041	n.s.	Age*Ped-near	-0.010	-0.043	0.023	n.s.
Age*Ped-far	-0.050	-0.079	-0.021	<0.001	Age*Ped-far	0.038	0.005	0.071	n.s.
Age*Vehicle	0.022	-0.030	0.073	n.s.	Age*Vehicle	-0.011	-0.070	0.048	n.s.
Age*Boat	0.022	0.002	0.041	n.s.	Age*Boat	-0.004	-0.026	0.018	n.s.
Self-maintenance behavior					Vigilance behavior				
Ped-near	0.335	-0.056	0.726	n.s.	Ped-near	-0.181	-0.585	0.222	n.s.
Ped-far	-0.036	-0.439	0.368	n.s.	Ped-far	-0.293	-0.711	0.126	n.s.
Vehicle	0.012	-0.924	0.949	n.s.	Vehicle	0.957	-0.008	1.922	n.s.
Boat	0.037	-0.434	0.508	n.s.	Boat	0.175	-0.317	0.668	n.s.
Intraspecific	-0.035	-0.533	0.464	n.s.	Intraspecific	0.393	-0.112	0.899	n.s.
Temperature	-0.003	-0.011	0.004	n.s.	Temperature	0.002	-0.006	0.010	n.s.
Age	0.004	0.002	0.007	≤0.001	Age	0.005	0.002	0.007	≤0.001
Age*Ped-near	-0.022	-0.043	0.000	n.a.	Age*Ped-near	0.018	-0.004	0.040	n.s.
Age*Ped-far	0.001	-0.021	0.023	n.s.	Age*Ped-far	0.014	-0.009	0.037	n.s.
Age*Vehicle	-0.001	-0.044	0.033	n.s.	Age*Vehicle	-0.026	-0.066	0.014	n.s.
Age*Boat	-0.002	-0.017	0.013	n.s.	Age*Boat	-0.007	-0.022	0.009	n.s.
Foraging behavior					Locomotion behavior				
Ped-near	0.044	-0.344	0.433	n.s.	Ped-near	0.150	-0.208	0.507	n.s.
Ped-far	-0.208	-0.613	0.196	n.s.	Ped-far	-0.164	-0.528	0.200	n.s.
Vehicle	-0.991	-1.917	-0.064	n.s.	Vehicle	0.049	-0.809	0.907	n.s.
Boat	0.375	-0.106	0.855	n.s.	Boat	0.203	-0.216	0.621	n.s.
Intraspecific	0.014	-0.465	0.493	n.s.	Intraspecific	-0.346	-0.813	0.120	n.s.
Temperature	0.001	-0.006	0.009	n.s.	Temperature	-0.002	-0.008	0.005	n.s.
Age	0.000	-0.003	0.002	n.s.	Age	0.001	-0.001	0.003	n.s.
Age*Ped-near	-0.001	-0.022	0.021	n.s.	Age*Ped-near	0.003	-0.017	0.023	n.s.
Age*Ped-far	0.001	-0.021	0.023	n.s.	Age*Ped-far	-0.002	-0.022	0.018	n.s.
Age*Vehicle	0.042	0.004	0.080	n.s.	Age*Vehicle	0.002	-0.034	0.037	n.s.
Age*Boat	-0.011	-0.026	0.005	n.s.	Age*Boat	-0.009	-0.023	0.004	n.s.
Alarm behavior					Alarm behavior				
Ped-near	0.039	-0.118	0.195	n.s.	Age	0.001	0.000	0.001	n.s.
Ped-far	0.054	-0.098	0.206	n.s.	Age*Ped-near	0.000	-0.009	0.008	n.s.
Vehicle	0.672	0.302	1.042	≤0.001	Age*Ped-far	-0.007	-0.015	0.002	n.s.
Boat	-0.018	-0.188	0.152	n.s.	Age*Vehicle	-0.027	-0.042	-0.011	≤0.001
Intraspecific	0.719	0.514	0.924	≤0.001	Age*Boat	0.003	-0.002	0.009	n.s.
Temperature	-0.001	-0.004	0.002	n.s.					

[a]95% CI (CI_L = lower, CI_U = upper).
[b]Pedestrian ≤137 m of subject pair.
[c]Pedestrian 138-300 m from subject pair.
[d]Car, truck, or all-terrain vehicle ≤300 m of subject pair.
[e]Boat ≤300 m of subject pair.
[f]Extra-pair American Oystercatcher ≤300 m of subject pair.
[g]Days since hatching.

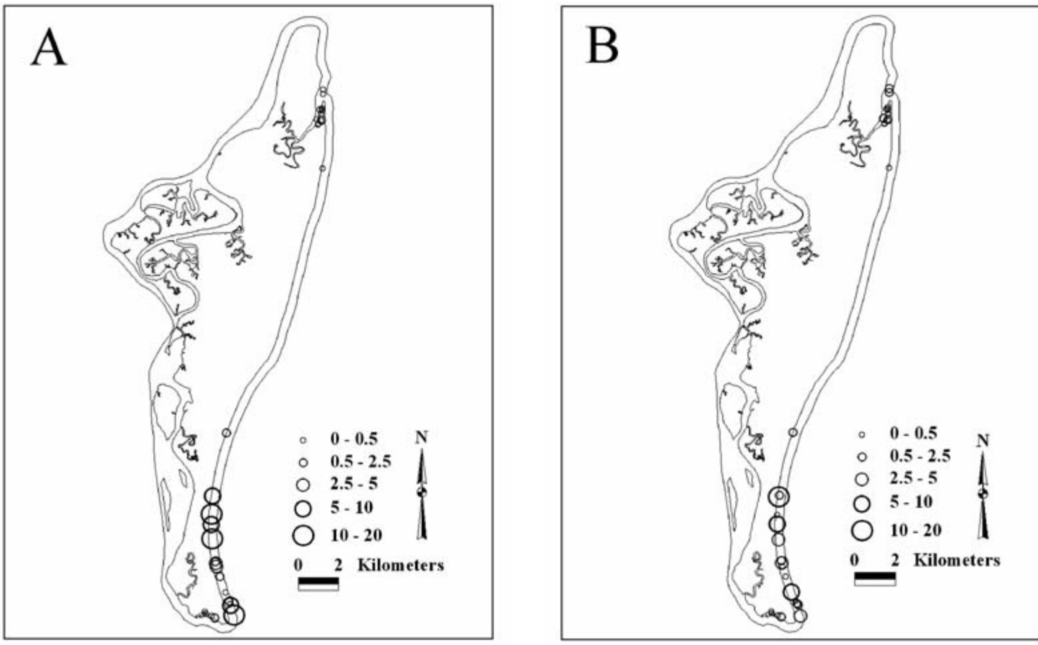

Figure 2. Locations of American Oystercatcher nests and their relative human disturbance on southern end compared to the undisturbed northern end, Cumberland Island National Seashore, Georgia, 2003-2004. The size of open circles represents the proportion of time disturbance was present for two disturbance types: (A) ped-near activity—pedestrian ≤137 m, and (B) ped-far activity—pedestrian 138-300 m of subject bird.

catchers at CINS during 2003 and 2004 breeding seasons. Data indicated that tide, temperature, intraspecific encounters, and human activity influenced oystercatcher behavior, such that reproductive success may have been affected negatively. Treatment of nest attempts as experimental units was considered appropriate because of the lack of information on individual identities of oystercatchers (within and between years) and because each nest attempt would have different disturbance scenarios unrelated to other attempts. There was no way to prove that the same pair or a different pair was involved in multiple nesting attempts. However, conservative test procedures with Bonferroni adjustments ($P < 0.005$) reduced possibilities of a Type II error.

At CINS, the frequency of occurrence of reproductive behavior during incubation was greater (64%) than for pairs in Virginia (female = 57%, male = 39%, N = 50; Nol 1985). The frequency of occurrence of self-maintenance, locomotion, vigilance, and alarm behaviors during incubation, as well as that of vigilance and alarm behaviors during brood rearing on CINS were similar to percentages reported for Virginia (Nol 1985). At CINS and Virginia, the frequency of occurrence of reproductive behavior decreased during brood rearing, but remained constant during incubation. Pairs allocated more time to foraging and vigilance behaviors when rearing chicks in Virginia and CINS (Nol 1985 and Fig. 1).

Tides, as expected, affected oystercatchers' behaviors. CINS pairs preformed more foraging and locomotion behavior during mid-falling than in other tidal phases in both incubation and brood rearing periods (Fig. 1), similar to data from other studies (Nol and Humphrey 1994). Oystercatchers fed on marine bivalves, mollusks, worms, and other marine invertebrates of coastal intertidal areas (Bent 1929; Tomkins 1947; Cadman 1980; Johnsgard 1981; J. B. Sabine, pers. obs.), which were more easily consumed when open and partially submerged during falling tides (Nol and Humphrey 1994). If foraging is optimal during mid-falling tides, then a corresponding reduction in reproductive behavior may be a consequence of foraging opportunity. In brood rearing, CINS pairs committed less time to vigilance behavior during

Table 4. Mean displacement rate and distance (m) from treatment stimuli in three disturbance experiments and effect from passing vehicles and all-terrain vehicles (ATV) for eleven nesting attempts of American Oystercatchers, Cumberland Island National Seashore, Georgia, 2004. Pedestrian (Ped) treatments showed no differences, but all caused displacement. Vehicles and ATVs had little to no effect.

Treatment	N	Proportion of displacement	Mean displacement distance (m)	95% CI (m)
Ped 20[a]	11	1.00	113.8	78.4-149.3
Ped 40[b]	10	0.78	118.3	99.9-136.6
Ped 60[c]	9	0.78	126.4	94.4-158.3
Vehicle[d]	9	0.00	NA	NA
ATV[e]	8	0.13	169.5	NA

[a]Observer walked by nest at 20-m seaward and parallel to beach.
[b]Observer walked by nest at 40-m seaward and parallel to beach.
[c]Observer walked by nest at 60-m seaward and parallel to beach.
[d]Observer drove by nest parallel to beach in a truck at high tide line (ca. 50 m from nest).
[e]Observer drove by nest parallel to beach on an all-terrain vehicle at high tide line (ca. 50 m nest).

mid-falling tides because of increased locomotion and foraging activity (Fig. 1).

In brood rearing, temperature may have caused changes in reproductive behavior, but not significantly. Reproductive behavior decreased as chicks aged (Table 3). During high temperatures, chicks needed more adult protection from thermal stress. Highly precocial oystercatcher chicks were most vulnerable to thermal stress shortly after hatching for one to two d; therefore, reproductive activity, as reported above, would be expected to be greater at an early age and decrease later (e.g., Welty 1975, p. 353).

Most pedestrians at CINS came by ferry and walked across the island to the beach during day trips. Therefore, pedestrian activities on the beach were concentrated near beach access trails closest to two ferry docks on the south end. Greater levels of human activity on the south end were attributed to additional visitors who came to the beach by private boats. Pedestrian activity decreased with distance from points of beach access. Human activities in more northern beach areas were limited to a few NPS employees, biologists, island residents, and few overnight campers and hikers.

Ped-near activity was most frequent during incubation, but decreased during brood rearing. This seems counterintuitive, because brood rearing (Jun-Jul) occurred concurrently with peak tourist season. Precocial oystercatcher chicks, however, can move within one to two d of hatching. The mobility of chicks releases the family group from the nesting territory and may enable the group to move from disturbed areas. Oystercatcher families moved 100-200 m from the nest to a tolerable distance from human activity at beach access trails and therefore would be disturbed less. Response to human activity was supported by an increase in reproductive behavior during ped-far activity in brood rearing (Table 3), which did not occur during incubation.

Pedestrian activity affected oystercatcher reproductive activity and possibly reproductive success on CINS. In Europe, oystercatchers devoted less time to incubation and foraging when disturbed on foraging grounds (Verhulst *et al.* 2001). This decline in reproductive behavior during incubation was also detected at CINS in response to ped-near events. Reduced nest attendance also may have reduced reproductive success on the south end of CINS (Sabine *et al.* 2006). At the south end, we documented higher predation rates than at the north end of the island, but we did not record delayed fetal development (Vleck and Vleck 1996).

Incubating oystercatchers on CINS did not alter behaviors in the presence of ped-far activity, but did alter behavior in the presence of ped-near activity, indicating that response to human activity was negatively correlated with distance between nests and pedestrians. Where ped-near activity was frequent, we documented nest abandonment and direct human destruction of nests. Negative correlations between reproductive success and frequencies of and distant to pedestrian disturbances have been documented also for other waterbird species (Hunt 1972; Burger 1981; Burger and Gochfield 1998; Verhulst *et al.* 2001; Rodgers and Schwikert 2003).

During incubation vehicle disturbances resulted in increased reproductive, decreased self-maintenance, and decreased vigilance behaviors. These behavioral responses suggest that during vehicular disturbances, oystercatchers' strategy was to avoid behavior that would attract attention (i.e., remain motionless on eggs). These behavioral responses to vehicles during incubation would be beneficial to clutches, and ultimately to hatching success. During brood rearing, however, foraging behavior decreased during disturbances by vehicles, which could reduce food for chicks. In a similar situation, Eurasian Oystercatchers allocated fewer food resources to chicks when disturbed while foraging (Verhulst *et al.* 2001). Reduced foraging of oystercatchers caused by vehicular activity during brood rearing may have negative impacts on chick survival depending on the number and time of vehicular disturbances, especially during important foraging times, such as falling tides.

Boat activity had no effect on oystercatcher behavior during incubation or brood rearing on CINS. In Florida, however, wading bird nesting experiments involving motorized boats indicated that 60-90 m buffer zones were needed to reduce disturbance (Rodgers and Smith 1995). The differences may be related to passing boats on CINS and approaching boats in the Florida study. Nesting terns in New Jersey, however, were disturbed by motorboats and personal watercraft (PWC), which resulted in recommendations of 100-m buffer for PWC and significant reductions in PWC speed to reduce noise (Burger 1998).

Oystercatcher nests failed primarily because of nocturnal nest predation by mammals during incubation (Sabine *et al.* 2005, 2006). Human activity was minimal at night (≤1 group/night [21.00-23.00 h], J. B. Sabine, pers. obs.) and nocturnal turtle surveys did not occur as in the past (Rappole 1981). We found no evidence that diurnal nest predation events were related to direct human activity; therefore, this study did not support the hypothesis that disturbance increases parental activity, which in turn 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 from disturbance experiments in this study supported the prevailing hypothesis that during incubation, ground-nesting birds are more likely to leave their nests when disturbances come from pedestrian rather than vehicles (Vos *et al.* 1985; Klein 1993; Rodgers and Smith 1995). Furthermore, results indicated that vehicular activity affected pairs differently during incubation and brood rearing, which will require different management approaches to conservation of nesting habitat for oystercatchers.

Variation within and among species of waterbirds is common in response to human activities (Anderson 1988; Erwin 1989; Rodgers and Smith 1995, 1997; Burger 1998; Rodgers and Schwikert 2002, 2003). Data from this study supported this variation, with displacement distances (distance when bird left nest) from pedestrian disturbance varying from 27 to 319 m. Although highly variable, the mean displacement distances among our pedestrian disturbance treatments were equal and fairly consistent (Table 4, 114-126 m) and agreed with no-disturbance zone recommendations (distance from nest for pedestrians) for similar species. Rogers and Smith (1995) recommended pedestrian no-disturbance zones of 178 m for Black Skimmer (*Rynochops niger*) colonies and 154 m for least tern colonies. In Virginia and North Carolina, terns and skimmers flushed at mean distances of 106-142 m when two pedestrians approached colonies from the berm of the intertidal zone (Erwin 1989). The number of successful oystercatcher nesting pairs should increase with the establishment of no-disturbance zones around nests at CINS.

MANAGEMENT IMPLICATIONS

Differences in behavioral responses between ped-near and ped-far activities during incubation indicated that negative effects of disturbances by pedestrians are reduced with increasing distance. At CINS, a good approximation of American Oystercatchers' tolerance to human activity during incubation would be 137 m. Managers at CINS should consider this distance when establishing no-disturbance zones and expand but not contract the zone. Behavioral responses to ped-near and ped-far activity during brood rearing were mixed, but suggest that disturbance distance increased during brood rearing; therefore, pedestrian-free zones of ≥150 m (including closure of beaches in high traffic areas) may be appropriate during brood rearing. When establishing pedestrian-free zones, managers should provide information to educate the public about nesting oystercatchers as well as other waterbird nesting colonies in the area and should encourage pedestrians to move past nesting areas in the intertidal zone quickly if pedestrian-free zones are established on open beaches.

Although presence of vehicular activity altered behavior during incubation, reproductive behavior was not impacted negatively, suggesting that vehicular activity, at its 2003-2004 levels at CINS, did not affect hatching success. During brood rearing, however, foraging behavior was lower in the presence of vehicular activity, which may alter chick provisioning and ultimately chick survival. Radio-marked chicks in future studies may be helpful in determining their survival. We recommend some prohibition of beach driving in areas of dense oystercatcher territories when chicks are present (late May to late Jul) at CINS. Continual monitoring of oystercatcher reproductive success would be necessary to determine effectiveness of pedestrian- and vehicular-free zones.

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