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Source: The Condor, 116(4):588-598. 2014.
Published By: Cooper Ornithological Society
DOI: http://dx.doi.org/10.1650/CONDOR-14-35.1
URL: http://www.bioone.org/doi/full/10.1650/CONDOR-14-35.1

THE CONDOR
Ornithological Applications
www.cooper.org

Volume 116, 2014, pp. 588–598
DOI: 10.1650/CONDOR-14-35.1

RESEARCH ARTICLE

Reproductive ecology of American Oystercatchers nesting on shell rakes

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Submitted February 28, 2014; Accepted August 28, 2014; Published October 29, 2014

ABSTRACT
Degradation of nesting habitat for coastal birds has led to the use of nontraditional nesting habitat. The American Oystercatcher (*Haematopus palliatus*) is listed as a "Species of High Concern" by the U.S. Shorebird Conservation Plan and is declining in the southern portion of its U.S. breeding range, where ~50% of breeding oystercatchers nest on shell substrate instead of beachfront habitat. We measured daily survival rates during incubation and chick rearing in shell rake habitats over five breeding seasons in the Cape Romain region of South Carolina, USA. Of 354 nesting attempts monitored, 16.1% hatched at least one egg. During incubation, daily survival rate was 0.938, corresponding to 22.8% success to hatching (nest success). For broods, daily survival was 0.991, or 74.0% success from hatching to fledging. Productivity in the Cape Romain region is primarily being lost during the incubation phase, when nests are exposed to overwash and predation. Mobile chicks may, however, be able to avoid flood events or predators by relocating to higher or more protected portions of a shell rake. Based on comparative data for American Oystercatchers from elsewhere in their range, it does not appear that shell rakes in the Cape Romain region are inferior breeding habitat. Our data suggest that conservation actions targeting nest and chick loss from flooding and predation have the greatest opportunity to enhance reproductive success in this core breeding area, and that an assessment of the availability, structure, avian use, and protection status of shell rakes is warranted.

Keywords: American Oystercatcher, Cape Romain, daily survival rate, flooding, *Haematopus palliatus*, predation, reproductive success, South Carolina

Ecología reproductiva de individuos de *Haematopus palliatus* que anidan sobre sustrato de conchas

RESUMEN
La degradación del hábitat de anidación de aves playeras las ha llevado a usar hábitat no tradicional para anidar. *Haematopus palliatus* está clasificada como una "especie de alto interés" por el plan de conservación de aves playeras de EEUU y sus poblaciones han disminuido en la parte sur de su distribución reproductiva, donde ~50% de las aves anidan sobre restos de conchas en vez de en la playa. Medimos las tasas de supervivencia diaria durante la incubación y la cría de los polluelos en los hábitats con sustrato de conchas por cinco temporadas reproductivas en la región de Cape Romain en Carolina del Sur, EEUU. De 354 intentos de anidación monitoreados, en 16.1% eclosionó al menos un huevo. Durante la incubación, la tasa diaria de supervivencia fue 0.938 y la probabilidad de éxito de los nidos fue solo 22.8%. Para las nidadas, la tasa diaria de supervivencia fue 0.991 y la probabilidad de éxito de los nidos fue 74.0%. La productividad en la región de Cape Romain se pierde principalmente durante la fase de incubación, cuando los nidos están expuestos al flujo de sedimentos y a la depredación. En cambio, los polluelos podrían ser capaces de moverse para evitar eventos de inundación o depredadores, reubicándose en porciones más altas y protegidas del sustrato de conchas. Con base en datos comparativos sobre *H. palliatus* en otras partes de su distribución, no parece que los sustratos de conchas en la región de Cape Romain sean inferiores en relación con otros hábitats de reproducción. Nuestros datos sugieren que las acciones de conservación cuyo objetivo sea evitar la pérdida de nidos y polluelos por inundaciones y depredación tienen la mayor probabilidad de mejorar el éxito reproductivo en esta área central de reproducción. Además, nuestros datos indican que se justifica hacer una evaluación de la disponibilidad, estructura, uso por parte de aves y estado de protección de las áreas con restos de conchas acumulados.

Palabras clave: Cape Romain, Carolina del Sur, depredación, éxito reproductivo, *Haematopus palliatus*, inundación, tasa de supervivencia diaria

INTRODUCTION

Numerous species of North American breeding bird that nest on beaches and in coastal ecosystems of the southeastern U.S., such as the Piping Plover (*Charadrius melodus*), Wilson's Plover (*Charadrius wilsonia*), American Oystercatcher (*Haematopus palliatus*), Least Tern (*Sternula antillarum*), and Black Skimmer (*Rynchops niger*), have experienced loss or degradation of nesting habitat, raising concern about their population stability (Brown et al. 2001). For some species, habitat loss has been accompanied by use of nontraditional nesting habitat, perhaps due to both unsuitability of traditional nesting sites and creation of new, apparently suitable habitat. For example, Least Terns and Black Skimmers now readily nest on rooftops throughout the southeastern U.S. (Gore 1987, Krogh and Schweitzer 1999, Cameron 2008). Although birds may initiate nesting in these nontraditional habitats, reproductive success may not be equivalent to that experienced in traditional habitat. For example, a novel habitat may appear adequate for nesting, but instead may function as an ecological trap due to some proximal factor that leads to increased mortality of nests, chicks, or adults.

The American Oystercatcher (hereafter, oystercatcher) is listed as a "Species of High Concern" by the U.S. Shorebird Conservation Plan (Brown et al. 2001). Like other species of shorebird that nest on beaches in North America, oystercatchers are threatened by disturbance and development on their nesting grounds (McGowan and Simons 2006, American Oystercatcher Working Group et al. 2012). In the mid-Atlantic and south Atlantic U.S. states, the species has declined in abundance, particularly on barrier islands that previously supported nesting (Davis et al. 2001, Wilke et al. 2005). However, the species demonstrates plasticity in choice of nesting habitat and uses dredge spoil islands, marshes, rooftops, and forests (Froling 1965, Lauro and Burger 1989, Shields and Parnell 1990, Toland 1992, McGowan et al. 2005, Florida Fish and Wildlife Conservation Commission 2011). Within the mid-Atlantic and south Atlantic U.S. states, oystercatchers also nest and raise chicks on washed shell rakes. For example, 35–50% of oystercatcher nests in Virginia, South Carolina, Georgia, and Florida occur on shell rakes (Douglass and Clayton 2004, Wilke et al. 2005, Sanders et al. 2008, T. Keyes personal communication). These rakes are narrow fringes of shells, primarily of eastern oysters (*Crassostrea virginica*) and blue mussels (*Mytilus* spp.), that accrete by wind and wave energy along shorelines, typically between marshes and open water (Figure 1). The lower elevations of shell rakes may be intertidal or prone to overwash by waves, while higher elevations may be less affected by regular tide fluctuations or minor wave activity. Shell rakes form within the range of eastern oysters and blue mussels, and, while certain areas appear to favor the formation of shell rakes, the exact location, elevation, and extent of rakes tend to be dynamic among years.

Few other species in the mid-Atlantic and south Atlantic U.S. states nest or raise chicks on shell rakes, suggesting that oystercatchers may be uniquely exploiting this habitat. Shell rakes do, however, support a variety of birds (primarily for foraging and loafing), mammals, fish, and invertebrates. Despite their ecosystem services, shell rakes have been little studied, and their distribution has only recently begun to be mapped (Coen et al. 2007). For example, in South Carolina, USA, where ~56% of oystercatcher nests occur on shell rakes, preliminary analyses have enumerated ~6,330 shell rakes totaling 2 million m^2 (www.dnr.sc.gov/GIS/descoysterbed.html). Approximately 27% of these rakes occur in the Cape Romain region, an estuarine–marine system along the central coast. The Cape Romain region also supports ~60% of the 400 breeding pairs of oystercatchers in South Carolina, representing ~15% of the breeding population within North America (American Oystercatcher Working Group et al. 2012).

Our goal was to assess the reproductive success of oystercatchers on shell rakes in the Cape Romain region (Figure 2), a core portion of the species' breeding range. Our objectives were to measure daily survival rates during incubation and chick rearing and to determine causes and timing of nest failure. We conducted our study during five breeding seasons (2006–2008 and 2010–2011). We focused our research along the Atlantic Intracoastal Waterway (AICW) and along the shores of Bulls Bay (Figure 2), two areas that may present different overwash and predation regimes because of their differing locations and physical characteristics. The AICW borders the mainland on its landward side. Its shell rakes form due to boat wakes. Bulls Bay is separated from the mainland by the AICW and a matrix of salt marshes and tidal creeks. Shell rakes here form due to natural wind and wave activity. Our research represents the first study of breeding oystercatchers that focuses explicitly on shell rakes, and provides a basis for evaluating reproductive success in this commonly occurring habitat type.

METHODS

Study Area

The Cape Romain region, which extends from the Cape Romain National Wildlife Refuge south to the Isle of Palms in South Carolina (Figure 2), is comprised of barrier islands, shallow bays, tidal creeks, salt marshes (dominated by *Spartina alternaflora*), mudflats, and eastern oyster shell reefs. The AICW, a 100–300 m wide channel that is maintained for boat traffic, also is a dominant feature of the region. In South Carolina, the AICW was completed in

FIGURE 1. A typical shell rake along the Atlantic Intracoastal Waterway (AICW) in the Cape Romain region, South Carolina, USA. Shell rakes in this area tend to be long and narrow, bordered by water on one side and salt marsh on the other, and provide breeding habitat for American Oystercatchers. Photo credit: J. M. Thibault

the 1940s (Parkman 1983) and hence has been available as nesting habitat for oystercatchers for at least 70 years.

We examined reproductive success on shell rakes along a 12.6 km length of the AICW from channel marker 67 (west of Bulls Bay) to marker 96 (west of the southern end of Dewees Island) and also along the southwestern edge of Bulls Bay from Venning Creek to the Bull Island Channel (Figure 2). Bulls Bay is a shallow tidal bay (0.15–2.70 m deep) within the Cape Romain National Wildlife Refuge and is separated from the mainland by extensive *Spartina* salt marsh. In the AICW, shell rakes are formed primarily by waves from boat wakes and are interspersed along the channel edge. In contrast, shell rakes in Bulls Bay are formed along the shore primarily by winter storms (Sanders et al. 2008). In our study area shell rakes tend to be long (50–150 m), narrow (1–3 m), low-elevation (0.5–1.5 m) structures that are bordered by water and salt marsh. The region is characterized by a bimodal tidal cycle, with tidal changes as great as 2.5 m during spring tides.

Oystercatchers in the region typically initiate nesting in early April. Nests that occur on shell rakes are shallow depressions. Clutch size is typically 1–3 eggs, with a 27-day incubation period. Replacement clutches following nest loss are common. Although precocial, oystercatcher chicks are provisioned by parents until and sometimes after fledging, which occurs $\sim$35 days after hatching. Once mobile, chicks in our study areas occupy the nesting territory from the edge of the water to the marsh border, occasionally using the marsh for cover. Older chicks may forage on intertidal reefs at the edges of nesting territories. Parents forage during low tide on exposed, intertidal, live reefs, which may occur on the edges of nesting territories or which may require adults to commute (Thibault et al. 2010, Hand et al. 2010).

Nest and Chick Monitoring

We monitored shell rakes from late March until mid-July in 2006–2008 and 2010–2011. Shell rakes were checked

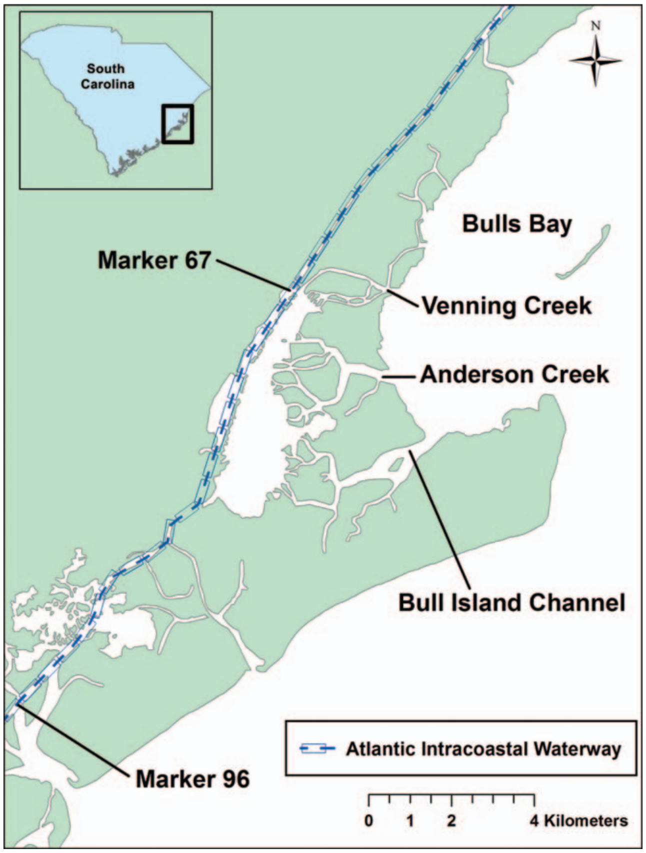

FIGURE 2. Study area within the Cape Romain region, South Carolina, USA. Study nests of American Oystercatchers occurred along the Atlantic Intracoastal Waterway (AICW) between markers 67 and 96, and in southwestern Bulls Bay (SWBB) between Venning Creek and the Bull Island Channel.

for signs of breeding oystercatchers by boat and on foot every 2–3 days on average. Oystercatchers on shell rakes are very visible when incubating. Their black-and-white plumage stands out against the bright white shells of rakes, and rakes tend to be narrow and free of vegetation. Oystercatchers often vocalize when humans approach, further enhancing detectability. Nonetheless, it is possible we missed nests or renests; hence, our estimates of each should be viewed conservatively. Data from the 2010 and 2011 breeding seasons were collected as part of another study that required a portion of nests to be treated as experimental nests for artificial incubation (Collins 2012). Here we use data from control nests only in 2010 and 2011, which were treated identically to nests during 2006–2008.

When a nest was discovered, we recorded its location using a handheld GPS (accurate to $\pm$3 m), the number of eggs present, and the band combinations of any adults observed at the nesting territory. We buried plastic cups (350 ml) near each nest to record flood events (Brooks et al. 2013). These washover cups were oriented horizontally to and parallel with the nest bowl, had lids to prevent rainwater from entering the cup, and contained holes along the edge that allowed salt water to collect in the bottom of the cup when flooding occurred. Nests were monitored at $\sim$3-day intervals until the eggs hatched or until the nest failed. During 2008 and 2011 cameras were also used opportunistically to determine nest fate. We considered a nest successful if $\geq$1 egg hatched. Causes of nest failure were classified as abandoned (eggs were cold and/or moisture was seen on the eggshells), adult mortality (one or both adults died during incubation and eggs failed to hatch), human disturbance (the nest was destroyed due to human activity), failure to hatch (hatching didn't occur although parents continued to incubate through subsequent nest observation intervals), overwashed (the overwash cup adjacent to the nest contained saltwater or was dislodged from the shell mound, eggs were missing and wrack debris had accumulated at the nest site since the previous nest check, or eggs were located in wrack debris), depredated (signs of predation were seen, such as broken eggshells, disturbed nest, yolk stains, and/or predator tracks or scat at or near the nest), or unknown (empty scrapes were observed prior to the estimated hatching date and no signs of predation or overwash were evident). We continued to monitor all shell rakes within the study site throughout the study period for signs of renesting by pairs whose nests had failed. The majority of nesting pairs (ca. 73%) in this study had at least one uniquely banded adult. We continued to monitor territories with successful nests at $\sim$3-day intervals to assess brood survival. We considered a brood successful if $\geq$1 chick fledged. Chicks were considered "fledged" at 35 days or when observed in flight. Where possible we classified causes of chick loss based on field signs, but we did not analyze these ad hoc data.

Statistical Analyses

We used logistic exposure models (Shaffer 2004) and a model selection approach to examine daily survival rates (DSR) of nests and broods. A set of a priori models was constructed (Appendix A), including a global model and a constant survival (intercept-only) model. Models tested various hypotheses, including, but not limited to, environmental variation, nesting status, nest location in relation to potential disturbance factors, and potential food availability. The following explanatory variables were considered for DSR of nests and broods: year, maximum tide height (maximum during interval between visits; established using Tidelog Southeastern Edition, Pacific Publishers, Bolinas, California, USA), day of the nesting season (and its squared value), age of the nest measured as days after the first egg was laid (and its squared value), site (AICW or Bulls Bay), location within site (AICW west, bordering the mainland; AICW east, separated from the mainland by the AICW; Bulls Bay north, north of Anderson Creek; Bulls

TABLE 1. Reproductive effort of American Oystercatchers in the Cape Romain region, South Carolina, USA, 2006–2008 and 2010–2011. AICW = Atlantic Intracoastal Waterway, SWBB = southwestern Bulls Bay.

Site	Year	No. pairs	No. nest attempts	No. successful nests	No. chicks fledged	No. chicks per pair
AICW	2006	35	71	14	10	0.28
	2007	30	67	4	2	0.07
	2008	27	44	12	11	0.41
	2010	17	31	6	10	0.59
	2011	13	24	3	5	0.38
SWBB	2006	18	24	10	16	0.89
	2007	16	38	2	0	0.00
	2008	15	20	5	6	0.40
	2010	8	18	1	1	0.12
	2011	8	17	0	0	0.00
All		187	354	57	61	0.33

Bay south, south of Anderson Creek), individual shell rake (16 rakes within AICW east, 3 within AICW west, and 5 each within Bulls Bay north and south), areal extent of intertidal shellfish reefs (i.e. potential foraging habitat) within 50 m (ha50) and 500 m (ha500) of each nest territory (South Carolina Department of Natural Resources 2010), and observer intensity (the number of days between visits to the nest site).

We ranked each model based on its Akaike Information Criterion value adjusted for small sample size (AIC_c; Burnham and Anderson 2002). Regression coefficients from the most-supported model were used to estimate DSR for various values of the explanatory variable(s). For each model, we calculated the difference in AIC_c value from the most-supported model (ΔAIC_c) and the AIC_c model weight (w_i). Models separated by $\Delta AIC_c < 2$ were considered to be equally supported (Burnham and Anderson 2002). We present models with $w_i > 0.10$. Coefficients were converted to odds ratios to allow for additional interpretation. Nest success (the probability of a nest surviving from egg laying to hatching) and brood success (the probability of at least one chick surviving from hatching to fledging) were calculated as the DSR from the most-supported model raised to an exponent equal to the number of days in each reproductive stage (27 days for incubation and 35 days for fledging).

We measured the extent of exposed intertidal reefs within 50 m and 500 m of each nest site to represent the availability of adjacent foraging habitat (www.dnr.sc.gov/GIS/descoysterbed.html, Hand et al. 2010, Thibault et al. 2010). An ANOVA was used to determine (1) the relationship between the day within the nesting cycle that a nest was lost and the independent variables site (AICW or Bulls Bay) and year, and (2) differences in areal extent of exposed shellfish reef (i.e. foraging habitat) within 50 m and 500 m of each nesting territory between sites (AICW or Bulls Bay). We used a logistic regression model to determine whether the proportion of nests lost to overwash compared with predation differed among sites and years. We did not include data from 2011, when cameras were deployed at nest sites and hence the likelihood of attributing nest loss to predation may have increased.

For all analyses, P-values are reported. Means and coefficient estimates are presented ± 1 standard error unless stated otherwise.

RESULTS

Nesting Ecology and Habitat

The duration of nesting activity (the time from when the first egg in the population was laid until the last chick fledged) ranged from 106 to 119 days among the five survey years. The earliest that nesting was initiated in any year was on April 1 (2008) and the latest nest was initiated on June 22 (2007). We made 1,662 observations of 354 nesting attempts by 187 pairs at a mean frequency of one nest check per 2.70 $\pm$ 0.07 days (Table 1). Pairs averaged 1.60 $\pm$ 0.04 (range: 1–4) clutches per season. Additional clutches occurred only after nest failure. Pooled across all nesting attempts, 18% of clutches contained one egg, 44% contained 2 eggs, 35% contained 3 eggs, and 3% contained 4–6 eggs, with the 6-egg clutch occurring in a communal nest (also see Lauro et al. 1992 and Sanders et al. 2008 for evidence of communal nesting in oystercatchers).

The areal extent of intertidal reefs within 50 m of the nest territory was greater ($F_{1,339} = 18.5$, $P < 0.001$) in Bulls Bay (0.04 $\pm$ 0.03 ha) than in the AICW (0.02 $\pm$ 0.03 ha). The areal extent of intertidal reefs within 500 m of the nest site also was greater ($F_{1,339} = 25.6$, $P < 0.001$) in Bulls Bay (1.57 $\pm$ 0.54 ha) than in the AICW (1.12 $\pm$ 0.80 ha). There was no correlation between the areal extent of exposed reefs within 50 m and 500 m of each nest site ($r = 0.08$). Within the AICW, 47% of nesting attempts had no exposed reefs within 50 m of the nest site, although all nesting attempts had 0.18–4.25 ha of exposed reef within 500 m of the nest site. Within Bulls Bay, 9% of nesting attempts had no exposed reefs within 50 m of the nest site,

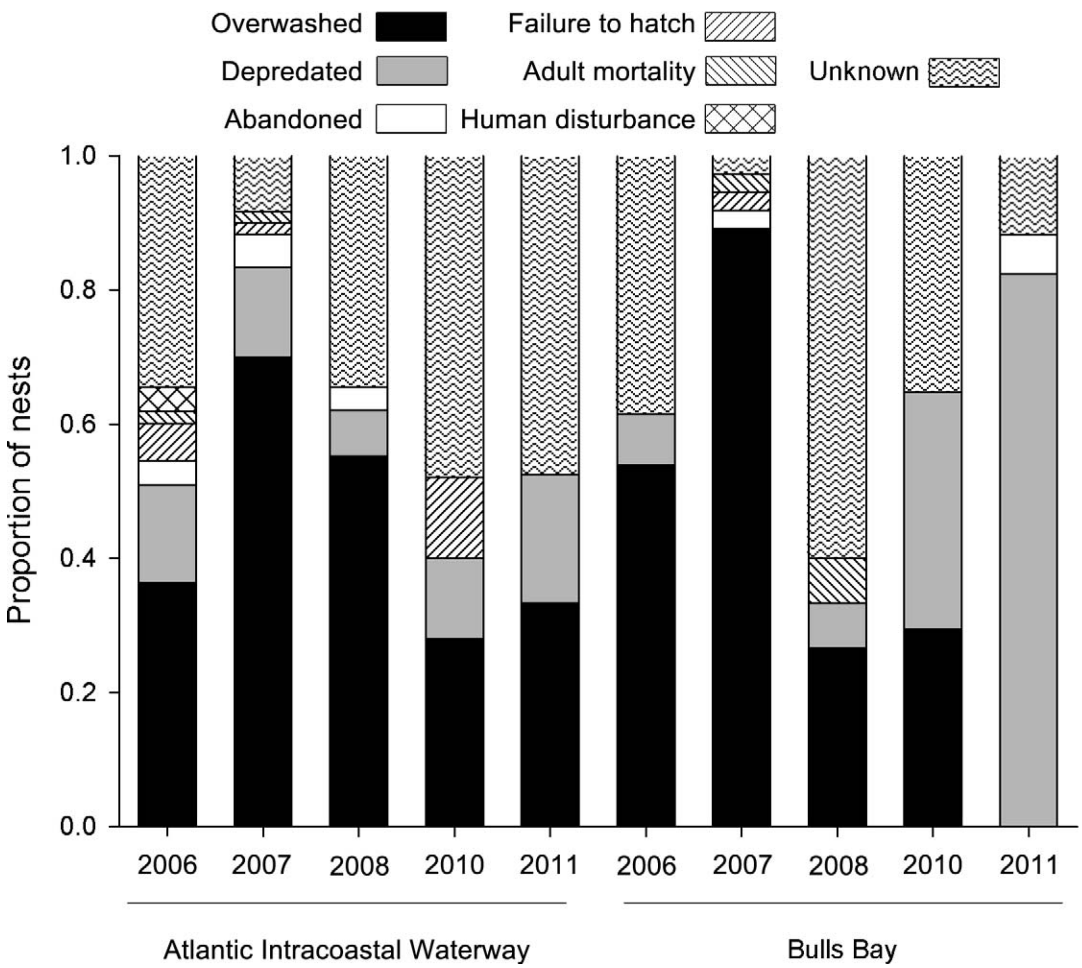

FIGURE 3. Causes of failure of American Oystercatcher nests within the Cape Romain Region, South Carolina, USA, in 2006–2008 and 2010–2011. The number of nests monitored by site and year appear in Table 2. Causes of failure are defined in the Methods.

although all nesting attempts had 0.57–2.65 ha of exposed reef within 500 m of the nest site.

Reproductive Success and Daily Survival

Of the 354 nesting attempts that we monitored, 57 nests (16.1%) hatched at least one egg (Table 1). The major identifiable cause of nest loss in most years and locations was overwash of nests (Figure 3). Although no nests were lost to overwash in Bulls Bay in 2011, overwash accounted for 27–89% of nest loss in other years at both sites. Similarly, although no nests were lost to predation in Bulls Bay in 2007, predation accounted for 7–82% of nest lost in other years at both sites. The odds of a nest being lost to predation compared with flooding did not differ by site ($\chi^2_1 = 1.4$, $P = 0.2$), but did differ among years ($\chi^2_3 = 13.2$, $P = 0.004$). The odds of a nest being lost to predation compared with flooding in 2006 compared with 2010 increased 7.7 times (95% CI = 2.4–24.7). The mean (± SD) age at which nests were lost was 11.5 ± 7.3 days. Nest loss was most common between nest days 7 and 13 (47.5% of nests lost) and relatively similar during the first week of incubation and after the second week of incubation (ca. 25% of nests lost each period). Timing of nest loss did not differ by site ($F_{1,279} = 0.4$, $P = 0.5$), but did occur earlier in 2010 (6.5 ± 4.4 days) and 2011 (7.6 ± 5.3 days) compared with 2006–2008 (11.8 ± 5.6 days; $F_{4,279} = 4.0$, $P < 0.001$).

There was an adequate fit between the observed survival data for nests in the incubation stage and the global model. The estimated $\hat{c}$ based on the global model was 0.81. Three models had $w_i > 0.10$ (Table 2). The best-supported model included only maximum tide height ($w_i = 0.53$; coefficient estimate ± SE from best model = –3.07 ± 0.42). Maximum tide height + site was also supported ($w_i = 0.30$), as was maximum tide height plus nest age and seasonal effects ($w_i = 0.10$). The odds of a clutch surviving increased 21.5 times for each 1 m decrease in maximum tide height during the observation

TABLE 2. Model selection results for daily survival rate of American Oystercatcher nests and broods in the Cape Romain region, South Carolina, USA, in 2006–2008 and 2010–2011. Models are ranked by ascending value of difference in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c), with the most-supported model at the top of the list. K = the number of parameters in each model, Dev is the deviance, ΔAIC_c is the AIC_c value relative to the highest-ranked model, w_i = Akaike weight (likelihood of being the best model), and Cumulative sum of w_i is the sum of Akaike model weights. Only models with $w_i > 0.10$ are presented.

Breeding stage and model parameters	K	Dev	ΔAIC_c	w_i	Cumulative sum of w_i
Nest survival					
Maximum tide height [a]	2	1337.0	0.0	0.53	0.53
Maximum tide height + Site	3	1336.2	1.2	0.30	0.83
Maximum tide height + Nest age + Nest age^2 + Season day + Season day^2	6	1331.8	2.7	0.13	0.96
Brood survival					
Site + Year [b]	3	94.3	0.0	0.65	0.65
Year	2	99.3	3.5	0.11	0.76

[a] The AIC_c value of the best model (Maximum tide height) = 1341.0.
[b] The AIC_c value of the best model (Site + Year) = 106.2.

interval. Except for tide height, all other variables in the three highest-ranked models had coefficient estimates with 95% confidence intervals that included zero; hence, the relationships between DSR and site, nest age, and day of the nesting season are weak and uncertain. The daily survival rate and nest success for oystercatcher nests in all years and sites combined were 0.938 (95% CI: 0.415–0.997) and 22.8% (95% CI: 0.0–93.1%), respectively (Table 3).

Of the 57 successful nests, 40 (70.1%) fledged at least one young and ultimately produced 61 chicks (Table 1). Of the 40 successful broods, 22 fledged one chick, 15 fledged 2 chicks, and 3 fledged 3 chicks. Pooling across both sites for five years (i.e. 10 site-years), 187 pairs fledged 61 chicks from 354 nest attempts, resulting in a productivity estimate for the study period of 0.33 chicks per pair (range among both sites and all years: 0.00–0.89 chicks per pair; Table 1). Although it was difficult to discern cause of death, the majority of chicks that died (64.3%) did so within six days of hatching, while 13% died >20 days posthatching.

The estimated $\hat{c}$ based on the global model for brood survival was 0.3, indicating that the data were underdispersed, which is likely to result in conservative estimates of the effects of any independent variable on DSR (i.e. less likely to indicate an effect where one does not exist). Only two models were supported with $w_i > 0.1$ (Table 2). The best-supported model ($w_i = 0.65$) included site (coefficient estimate ± SE = –1.60 ± 0.80) and year (coefficient estimate <–23.2, SE < 1.4 for years 2006, 2007, 2008, and 2011 compared with 2010 reference level; Table 2). The odds of a brood surviving were 5.0 times greater in Bulls Bay than in the AICW, although fewer broods were monitored in Bulls Bay than in the AICW. The DSR for broods in Bulls Bay was 0.997 and brood success was 90.4%. In the AICW, the DSR for broods was 0.989 and brood success was 68.1%. Annually, the DSR and overall success for broods ranged from 0.990 and 71%

TABLE 3. Daily survival rate (DSR) of nests and broods of American Oystercatchers in the Cape Romain region, South Carolina, USA, 2006–2008 and 2010–2011. AICW = Atlantic Intracoastal Waterway, SWBB = southwestern Bulls Bay. DSR and success were calculated using the parameters from the best models (Table 2).

Site	Year	Nest DSR	Nest success	Brood DSR	Brood success
AICW	2006	0.945	25.3%	0.977	44.4%
	2007	0.941	25.4%	0.977	45.1%
	2008	0.930	20.7%	0.997	91.8%
	2010	0.938	21.3%	1.000	100.0%
	2011	0.939	23.4%	0.990	71.0%
SWBB	2006	0.934	20.0%	0.995	84.8%
	2007	0.928	19.0%	0.995	85.1%
	2008	0.924	18.1%	0.999	98.3%
	2010	0.941	24.3%	1.000	100.0%
	2011	0.940	23.1%	— [a]	— [a]
All		0.938	22.8%	0.991	74.0%

[a] There were no successful nests in SWBB in 2011.

(2011) to 1.000 and 100% (2010). Pooling all years and sites, the daily survival rate of broods was 0.991 (95% CI: 0.631–0.999) and brood success was 74.0% (95% CI: 0.0–99.4%; Table 3).

DISCUSSION

Nest Survival and Causes of Nest Loss

Determining daily rates of nest survival (as opposed to more basic and less accurate measures of apparent nest success) and causes of nest loss has been a priority for research on oystercatchers for the past decade (American Oystercatcher Working Group et al. 2012). The probability of a nest surviving to hatch at least one egg never surpassed 25% during our five-year study. The probability of hatching as determined by nest survival modeling has also been reported for oystercatchers nesting in North Carolina (28%, 852 nests, 15 years; Simons and Stocking 2011), New Jersey (14%, 205 nests, 2 years; Virzi 2008), and Georgia (45%, 32 nests, 2 years; Sabine et al. 2006). The relatively low level of nest success that we report appears to be consistent with data from the two larger-scale studies (i.e. >200 nests), and the relatively high level of interannual variability is consistent with data from the 15-year study in North Carolina.

Maximum tide height was the only variable that we assessed which had a strong effect on DSR of nests, and its negative influence on DSR of nests is consistent with the identification of flooding as the most common cause of nest loss (25–90% of nest failures in any site and year). Storms during late winter and early spring, as well as tropical storms during summer and autumn, can enhance tide heights substantially and result in flooding of shell rakes. In the Cape Romain region, spring tides in April and May can exceed 3 m and often coincide with the establishment of most first and second clutches (Thibault 2008). Along the AICW, vessel traffic passes by frequently and large wakes from barges and motor yachts can wash over entire shell rakes, dislodging eggs and even anchored boats. The quite consistent loss of nests to overwash throughout the breeding season suggests that these events are not restricted to either early- or late-nesting pairs. Flooding appears to be a common cause of nest failure for oystercatchers. Flooding and erosion were the primary causes of nest loss for oystercatchers on river islands in the Cape Fear region of North Carolina (McGowan et al. 2005). For pairs that continually failed in Virginia, nest loss occurred primarily from high water during spring tides (Nol 1989). Flooding and high tides also accounted for high proportions of nest loss in Black Skimmers and Least Terns nesting on beaches and shell islands in the Cape Romain region and for Wilson's Plovers nesting on beaches immediately north of Cape Romain (Brooks et al. 2013, 2014, Zinsser 2013) suggesting that oystercatchers are not uniquely subjected to overwash events in this region.

Predation was also a common cause of nest failure during our study, accounting for 7–82% of nest failure in 10 of 11 site-years. The higher frequency of predation in Bulls Bay in 2010 and 2011 may have been due to a combination of increased predation rates and better detection of predation (i.e. deployment of nest cameras in 2011). Observations of mink burrows and scat near oystercatcher nests in Bulls Bay in 2010 and 2011 suggested predator activity, and mink were also confirmed as nest predators at nearby colonies of Least Terns and Black Skimmers in 2009 and 2010 (Brooks et al. 2013, 2014). Furthermore, predation pressure may increase during high tides when mammalian predators vacate lower-elevation marshes, possibly adding a synergistic risk to the direct problem of flooding. In shell rake habitats, predation may be underrepresented as a cause of nest loss because field signs of mammal presence such as tracks and scat are difficult to detect. We documented American Crows (*Corvus brachyrhynchos*) and Laughing Gulls (*Leucophaeus atricilla*) depredating oystercatcher nests, but did not detect field signs that would have indicated predation as a cause of nest failure. To date, every assessment of breeding success of oystercatchers has identified predation as a common cause of nest loss (Schulte et al. 2010). For example, during eight years of monitoring, ca. 50% of nest failures on barrier island beaches in North Carolina were attributed to predation (McGowan et al. 2005). Sabine et al. (2006) also found that 65% of nest failures on Cumberland Island, Georgia, were due to predation. Both of these studies occurred on barrier island beaches, where field signs of predation may have been easier to detect than on the hard substrate in our field sites. Given the challenges of documenting predation compared with flooding at nests on shell rakes, we may be underrepresenting predation as a cause of nest failure and hence its importance to nest success in the Cape Romain region.

Brood Survival

Brood success was 74% over the duration of our study. Three other measures of brood survival are available for oystercatchers, all of which are considerably lower, ranging from 33% to 46% (Sabine et al. 2006, Murphy 2010, Simons and Stocking 2011). Although we monitored fewer broods in Bulls Bay, the odds of a brood surviving to fledge at least one chick were higher there than along the AICW. We posit that territory quality for chick rearing, which may include proximity and availability of prey (Nol 1989, Ens et al. 1992) as well as physical structure of the nest territory (e.g., elevation and slope; Hazlitt et al. 2002), is higher in Bulls Bay than in the AICW and subsequently has a positive effect on brood survival. For example, the availability of exposed shellfish reefs (i.e. foraging habitat) within 50 m and 500 m of nest sites is higher in Bulls Bay than along the AICW and this may contribute to territory quality. Thibault et al. (2010) suggested that higher levels of brood success for oystercatchers in the Cape Romain region were associated with higher levels of parental attendance, and that this relationship was positively affected by the areal extent of shellfish reefs adjacent to nesting territories (see also Ens et al. 1992). The physical attributes of nest territories also may have positively affected brood survival in Bulls Bay. Elevation of nest territories was higher and slope of the territory was less steep in Bulls Bay than in the AICW in the 2010 and 2011 breeding seasons, and there was a positive effect of elevation and a negative effect of slope on chick survival along the AICW in those years (Collins 2012). Nesting territories with higher elevations may limit the effects of overwash on mobile chicks, while steeper slopes may inhibit provisioning rates (Hazlitt et al. 2002). Nonetheless, the lack of a direct relationship between brood survival and the areal extent of shellfish reefs in this study suggests that food availability alone, at least as measured by the extent of shellfish reefs adjacent to nest sites, is not the sole mechanism driving this relationship. It appears more likely that a complex interaction of various factors such as food availability, microhabitat structure, and predation may be affecting brood survival. Our data suggest that these factors could vary among years, creating inconsistent patterns in brood survival. More direct measures of chick predation and provisioning would be valuable.

Shell Rakes and Conservation Planning

Shell rakes are an important and unique nesting habitat in a substantial portion of the breeding range of American Oystercatchers, a species of high conservation concern. In the Cape Romain region, nest success of oystercatchers breeding on shell rakes did not appear to be consistently lower than nest success on barrier islands in New Jersey, North Carolina, or Georgia (Sabine et al. 2006, Virzi 2008, Simons and Stocking 2011). Brood success, however, did appear to be higher on shell rakes in Cape Romain compared with brood success on barrier islands in Massachusetts, North Carolina, and Georgia (Sabine et al. 2006, Murphy 2010, Simons and Stocking 2011). We did not find a consistent difference in productivity between oystercatchers nesting on naturally formed rakes in Bulls Bay and those breeding on rakes formed from boat wakes along the AICW; it appears that productivity in both habitats was lost to natural flood events and predation pressure. Flooding from boat wakes appeared to be unique to the AICW, but it was not always possible to distinguish between anthropogenic and natural flooding events.

The American Oystercatcher Working Group identified seven management strategies to promote population stabilization and recovery of the species (Schulte et al. 2010), with four strategies focused on nesting: (1) identification of new nesting habitats (e.g., emerging alluvial sandbar islands), (2) protection of existing nesting areas through legal authorities, (3) creation or enhancement of nesting habitats, and (4) reduction of predation and human disturbance at nesting sites. In the Cape Romain region, objectives 1 and 2 are currently addressed through monitoring, protection, and outreach efforts led by state and federal agencies. Efforts to enhance shell rakes for nesting have met with limited success. For example, existing shell rakes in Cape Romain and Virginia were augmented with shell to raise elevation and reduce potential flooding; however, in neither case did birds select these experimental plots for nesting (Rounds et al. 2004, F. J. Sanders personal observation). Predator reduction targeted at mammals has been attempted intermittently in the Cape Romain region, with the objective of reducing nest loss for loggerhead sea turtles (*Caretta caretta*) and birds (National Marine Fisheries Service and U.S. Fish and Wildlife Service 2008, Collins 2012). Robust data are not available for oystercatchers, although anecdotal evidence suggests some level of success. Control efforts for avian predators are, however, more difficult to implement and maintain and also require substantial levels of permitting. Reduction of human disturbance at nest sites may be critical on beaches (American Oystercatcher Working Group et al. 2012), but the physical nature of shell rakes may serve as a natural deterrent to human activity. Rakes are difficult to access and currently offer little to no recreational or commercial opportunities; as such, they may provide a low-disturbance habitat for nesting and chick rearing by oystercatchers. An assessment of the availability, use, and protection of shell rake habitats throughout the species' range appears to be warranted, including a comprehensive comparison of reproductive success between shell rakes and other habitat types.

ACKNOWLEDGMENTS

We thank Ben Harris, Kate Goodenough, Christy Hand, Sarah Woodward, Billy Shaw, Charles Wahl, Adam DiNuovo, Nicholas Wallover, J. Benjamin Mongold, and Carolyn Wakefield for assistance with field logistics, data collection, and administration. We also acknowledge the support of Cape Romain National Wildlife Refuge; in particular, Sarah Dawsey, Matt Connolly, and Donny Browning. This research was supported by grants from The National Fish and Wildlife Foundation (Savannah Santee PeeDee Restoration Fund, Keystone Initiative) and the South Carolina State Wildlife Grants Program, as well as matching funds and support from the U.S. Fish and Wildlife Service, U.S. Geological Survey South Carolina Cooperative Fish and Wildlife Research Unit, and Clemson University. The manuscript benefited from comments by Conor McGowan and anonymous reviewers. Permits for various phases of this research were provided by the Clemson University Institutional Animal Care and Use Committee (protocols 2006-037 and 2010-028). The South Carolina Cooperative Fish and Wildlife Research Unit is supported by the South Carolina Department of Natural Resources, Clemson University, the U.S. Fish and Wildlife Service, and the U.S. Geological Survey. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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APPENDIX A. Logistic-exposure candidate models used in analysis of factors influencing daily survival rates (DSR) of nests and broods of American Oystercatchers in the Cape Romain region, South Carolina, USA, in 2006–2008 and 2010–2011. Variables are defined in Methods.

Models testing for null or global effect
- Null model [intercept only, constant survival]
- Global model [all main variables]

Models testing for effects of nesting location on DSR
- Site [coarse scale, 2 sites: Bulls Bay or AICW]
- Location within site [mesoscale, 2 locations within each site]
- Shell rake ID [finer scale, 19 rakes within AICW, 10 rakes within Bulls Bay]

Models testing for effects of environment on DSR
- Maximum tide height [flooding risk increases during higher tides]
- ha50 [areal extent of foraging habitat (exposed shellfish reefs) within 50 m of nest]
- ha500 [areal extent of foraging habitat within 500 m of nest]

Models testing for effects of date on DSR
- Year [interannual effects]
- Nest day + Nest day^2 [linear or nonlinear effect of nest age]
- Day in season + Day in season^2 [linear or nonlinear effect of date within year]

Models testing for effects of disturbance
- Observer effect [number of days between visits, frequency of researcher presence]

Models testing for multiple effects from above categories
- Site + Year
- Site + Maximum tide height
- Location within site + Year
- Maximum tide height + Location within site + Maximum tide height*Location within site
- Site + Nest day + Nest day^2 + Day in season + Day in season^2
- Maximum tide height + Nest day + Nest day^2 + Day in season + Day in season^2
- Location within site + Nest day + Nest day^2 + Day in season + Day in season^2
- Observer effect + Site + Nest day + Observer effect*Site + Observer effect*Nest day
- Site + Maximum tide height + Nest day + Nest day^2 + Day in season + Day in season^2 + Site*Maximum tide height
- Site + Year + Nest day + Nest day^2 + Day in season + Day in season^2 + Site*Year