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Source: Waterbirds, 33(4):511-517. 2010.
Published By: The Waterbird Society
DOI: 10.1675/063.033.0410
URL: http://www.bioone.org/doi/full/10.1675/063.033.0410

Parental Attendance and Brood Success in American Oystercatchers in South Carolina

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Abstract.—Research on breeding American Oystercatchers has focused on identifying factors that affect reproductive success but little attention has been paid to parent behavior during chick-rearing. Parental attendance of American Oystercatchers was measured in Bulls Bay and along the Atlantic Intracoastal Waterway (Waterway) within the Cape Romain Region, South Carolina, USA, during 2006. Parental attendance rates averaged 90.9% in Bulls Bay and 81.4% along the Waterway. Daily survival of chicks was higher in Bulls Bay (0.989 ± 0.007) compared to the Waterway (0.966 ± 0.012). The extent of shellfish reefs (i.e. foraging areas) adjacent to nest sites was greater in Bulls Bay (5,633 ± 658 m^2) compared to the Waterway (3,273 ± 850 m^2). Mean parental attendance in Bulls Bay was higher for successful broods (90.5%) compared to failed broods (79.8%). In contrast, mean parental attendance along the Waterway was higher for failed broods (93.4%) compared to successful broods (67.5%). Less extensive shellfish reefs adjacent to nest sites along the Waterway appeared to require parents to depart more frequently to forage and the resultant reduction in attendance may have negatively affected chick survival. Bulls Bay may provide higher quality nesting habitat compared to the Waterway with respect to proximity to food resources and parental attendance. Management and conservation efforts for American Oystercatchers should consider the relationship between foraging and nesting habitat and variability in behavioral attributes, such as parental attendance, in relationship to environmental conditions which ultimately affect reproductive success. *Received 10 November 2009, accepted 31 March 2010.*

Key words.—American Oystercatcher, Atlantic Intracoastal Waterway, brood survival, Cape Romain, *Haematopus palliatus*, parental attendance, South Carolina.

Waterbirds 33(4): 511-517, 2010

The American Oystercatcher (*Haematopus palliatus*) is listed as a species of high concern by the U.S. Shorebird Conservation Plan (Brown *et al.* 2001). There are approximately 1,500 nesting pairs along the Atlantic and Gulf Coasts of the U.S. (Brown *et al.* 2005) and the species appears to be declining in the southeastern portion of the range (Davis *et al.* 2001). South Carolina supports a substantial portion of the breeding population of American Oystercatchers in the southeastern U.S.A., approximately 400 pairs, and most of these breed within the Cape Romain National Wildlife Refuge (CRNWR) and areas adjacent (Sanders *et al.* 2008). The identification of causes of decline in American Oystercatchers has focused primarily on issues related to reproductive failure, particularly human disturbance and predation (McGowan and Simons 2006; Sabine *et al.* 2006). Parental attendance during chick-rearing has received little attention despite its potential to affect reproductive success.

Oystercatchers (*Haematopus* spp.) display an even partitioning of care between the sexes (Szekely *et al.* 2007) and have semiprecocial young which rely on parents for food prior to and after fledging (Nol and Humphrey 1994; Safriel *et al.* 1996). Therefore, parents must allocate time between biparental attendance (i.e. both parents present), single parent attendance, and leaving chicks unguarded. The proportion of time parents allocate between attending chicks and leaving them unguarded can affect the various compo-

nents of reproductive success. For example, chick growth and fledging success are related to the level and pattern of parental attendance during chick-rearing in Eurasian and North American Black oystercatcher (*Haematopus ostralegus* and *H. bachmani,* respectively; Ens *et al.* 1992; Hazlitt *et al.* 2002). However, to date, research that has considered parental attendance in American Oystercatchers has focused primarily on studies of the effects of human disturbance on parent behavior (McGowan and Simons 2006; Sabine *et al.* 2008) and therefore our understanding of this behavior is limited.

We examined parental attendance in American Oystercatchers in the Cape Romain region of South Carolina, U.S.A., as part of a larger research effort to understand factors that affect reproductive success of the species in a core portion of its range (Thibault 2008). We measured parental attendance during chick-rearing and brood success in an area where we suspected parents frequently foraged adjacent to nest sites but also in an area where we suspected parents commuted to forage. We sought to determine if differences between the two nesting areas in the juxtaposition of the food source to the nesting territory might mediate the relationship between attendance and brood success. Thus, we modeled our investigation on the resident/leapfrog model developed for Eurasian Oystercatchers (Heppleston 1972; Safriel 1985; Ens *et al.* 1992). Lastly, we examined the extent to which brood size, chick age, and nesting attempt affected parental attendance.

METHODS

Study Area

Parental attendance of American Oystercatchers (hereafter oystercatchers) was measured during the 2006 breeding season within the Cape Romain Region (CRR) of South Carolina (32°49'-33°05' N, 79°20'-79°45' W; Fig. 1) which includes the Cape Romain National Wildlife Refuge (CRNWR) and areas adjacent. The CRR supports a majority of the state's breeding oystercatchers (Sanders *et al.* 2008). Oystercatchers in the region nest primarily on elevated shell mounds and forage on shellfish reefs which were comprised primarily of eastern oysters (*Crassostrea virginica*) and ribbed mussels (*Geukensia demissa*). Oystercatchers were studied in Bulls Bay and along a section of the Atlantic Intracoastal Waterway (Waterway) (Fig. 1). Bulls Bay is a shallow tidal bay (0.15 m - 2.7 m deep) within CRNWR. Here, shell mounds formed along the shore primarily from winter storms. The Waterway is a deep channel which is maintained for boat traffic. Here, shell mounds formed primarily by waves from boat wakes and were interspersed along the channel edge (Sanders *et al.* 2008).

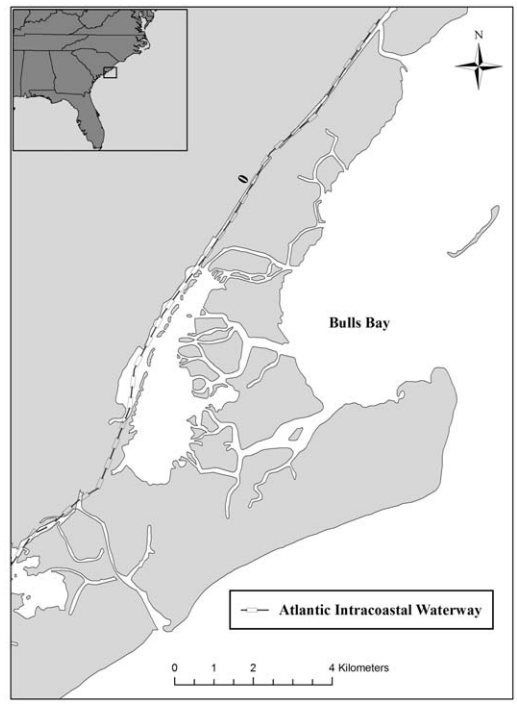

Figure 1. Study area within the Cape Romain Region, South Carolina, USA, May-July, 2006.

Field Procedures

Parental attendance was measured during the chick-rearing stage (18 May to 20 July 2006) during daylight hours and within ±2 hrs of low tide (i.e. when shellfish reefs were exposed and when adults foraged). Nests within Bulls Bay (n = 7 nests, n = 17 observations) and the Waterway (n = 6 nests, n = 22 observations) were numbered and observations were conducted on a rotating basis with additional nests added to the rotation as eggs hatched. Nests were observed one to five times during the chick rearing stage and this was considered in the statistical approach (see below). Observations were conducted either from a boat (both study areas) or land (Waterway only, opposite bank from nest) with observers 50 -100 m from nests. The mean width of shell rakes used for nest sites by oystercatchers in this study was 20.4 ± 2.6 m and this did not differ between the two habitat types ($t_7 = 2.3$, $P = 0.2$). Therefore, detection probability of chicks and adults was considered to be uniform between the two habitat types. We continuously recorded the presence of each adult and each chick during the observation period. If chicks were not observed during an observation period we searched the nest site during high tide when chick movement would be limited. The percentage of the observation period during which par-

ents were absent from the nesting territory or from shellfish reefs contiguous to and within 100 m of the nesting territory was then determined. The areal extent of shellfish reefs within 100 m of each nest was measured to determine if availability of adjacent foraging habitat differed between the two study areas (http://www.dnr.sc.gov/GIS/descoysterbed.html).

Statistical Analysis

We used chi-squared analyses to compare brood size and the number of nesting attempts between study areas and a t-test to compare the areal extent of adjacent shellfish reefs between study areas (i.e. one sample per nest). A t-test also was used to compare age of broods between study areas where each observation at each nest was treated as a sample (i.e. the age of the alpha chick was determined from its hatch date for each observation at each nest to allow for a comparison of ages between study areas during all surveys).

We used a mixed model with repeated measures (PROC MIXED, SAS Version 9.1, SAS Institute Inc., Cary, N.C., USA) to examine the percentage of time breeding adults were present at their territory during the low-tide foraging period. Nest identification was included as a random term and as the subject of the repeated measures statement. The proportion of total time attended in relation to total time available was the dependent variable. We combined the amount of time each parent was present at the nesting territory during the one-hour observation period to derive a measure of total attendance. For example, if parent 1 was on the territory for 50 min of a 60 min observation period, and parent 2 was on the territory for 40 min of the same 60 min observation period, then the percent time attended = ((50 + 40)/120)) = 0.75. Fixed factors included brood success (failed or ≥1 chick surviving to 35 days post-hatch; Yerkes 2000), brood size (1-3), nesting attempt number (1-3), chick age in days (d), and chick age^2 (allows for a nonlinear relationship between chick age and the dependent variable). We restricted this analysis to chicks ≤35 d post-hatch which is the estimated fledge date (Nol and Humphrey 1994). Two way interaction terms included in the model were chick age × brood size, and chick age^2 × brood size. We used a manual backward-selection process and deleted terms with $P > 0.10$ at each step. Percentages were transformed using the arc sine, square root transformation.

A mixed model with repeated measures was used to examine the difference in attendance times between parents (i.e. parent 1 attendance time - parent 2 attendance time) to assess possible compensation within pairs. Nest identification was included as a random term in the model and also was used as the subject of the repeated measures statement. The same factors, random variables, and procedures described above were used in this analysis.

The Mayfield method was used to calculate daily survival rate (DSR) during chick-rearing (Mayfield 1961). In order to obtain a larger sample size and a broader measure of DSR than afforded from the 'attendance nests', we also included nests from a larger sample that were being monitored for reproductive success but not attendance (Thibault 2008). Differences in DSR between locations were assessed with Z statistics (Johnson 1979).

Means are presented ± SE unless stated otherwise. Significance was set at alpha = 0.05 although actual P-values are reported throughout.

RESULTS

In Bulls Bay, 42% of 24 nest attempts fledged ≥1 chick while in the Waterway 20% of 71 nest attempts fledged ≥1 chick. DSR during chick-rearing was higher in Bulls Bay (0.989 ± 0.007) compared to the Waterway (0.966 ± 0.012; Z = 1.9, P = 0.03). Chick age and areal extent of reefs were both significantly greater in Bulls Bay compared to the Waterway (Table 1). The number of nesting attempts per nest site was greater along the Waterway due to more frequent clutch losses (Table 1). Based on the confounding nature of chick age, renesting effort, and areal extent of shellfish reefs with study area, we opted to analyze attendance data from each location separately.

Combined attendance of both parents at the nest site during low-tide periods ranged from 38% to 100% across study areas and observation periods. The weighted mean attendance for nests in Bulls Bay (90.9%) appeared to be higher compared to the Waterway (81.4%), although these were not compared directly due to the confounding

Table 1. Mean (SE) brood size (measured at start of observations), chick age (measured across all observations), number of nesting attempts, and areal extent of shellfish reefs within 100 m of nest sites for American Oystercatchers nesting along Bulls Bay or the Atlantic Intracoastal Waterway, Cape Romain Region, South Carolina, USA, May - July 2006.

Variable	Bulls Bay	Waterway	Test statistic, P-value
Chick age	28.4 ± 2.6	16.4 ± 1.9	$t_{37} = 3.8$, $P = 0.0005$
Extent of reefs (m^2)	5633 ± 658	3273 ± 850	$t_{11} = 2.2$, $P = 0.04$
Nesting attempts	1.2 ± 0.1	2.1 ± 0.2	$\chi^2 = 11.3$, $P = 0.003$
Brood size	1.7 ± 0.6	1.6 ± 0.8	$\chi^2 = 4.04$, $P = 0.13$

effects with study area. In Bulls Bay both parents were present for the entire observation period during 24% of samples and on the Waterway both parents were present for the entire observation period during 0% of samples.

On the Waterway, adult attendance at the nest site was most strongly related to brood success (Table 2) and this was the only variable to remain in the model throughout the backward selection process. Attendance was lower at Waterway nests that successfully fledged ≥1 chick compared to nests that failed to fledge any chicks (Fig. 2). In Bulls Bay, parental attendance also was related to brood success (Table 2). In contrast to the Waterway, attendance by parents in Bulls Bay was higher at nests that successfully fledged ≥1 chick compared to nests that failed to fledge any chicks (Fig. 2). Attendance also decreased in the brood from Bulls Bay with three chicks (only brood with three chicks during the study) as the chicks aged. There was no difference in attendance between adults within pairs in either location (P = 0.17 for both) and none of the variables tested had a significant effect on this relationship.

DISCUSSION

Parental attendance in oystercatchers was positively related to brood success in Bulls Bay but negatively related to brood success along the Waterway. The difference in the direction of this relationship between the two study areas may have occurred due to a trade-off between provisioning effort and attendance that was mediated by food location. We suggest that extensive shellfish reefs adjacent to nest sites in Bulls Bay allowed parents there to provision chicks without frequently needing to commute (i.e. reduce attendance) to forage. Because chick survival responds positively to provisioning and chick-guarding, a positive relationship between brood success and attendance likely developed. In contrast, parents along the Waterway were required to commute (i.e. reduce attendance) in order to provision chicks because nest sites there were adjacent to smaller areas of shellfish reefs. Because provisioning required a reduction in attendance in the Waterway, a negative relationship between brood success and attendance developed.

If the divergent relationships between parental attendance and brood success in our two study areas were caused by differences in the location of the food source in relation to the nest site, then our results would be consistent with the resident/leapfrog model demonstrated for Eurasian Oystercatchers (Heppleston 1972; Safriel 1985; Ens *et al.* 1992). Here, parents that commuted to forage (i.e. leapfrog nests) also allocated less time to attendance on the nesting territory and more time to food transport compared to parents that foraged adjacent to nest sites (i.e. resident nests). Also, reproductive success was subsequently lower in leapfrog nests compared to resident nests (Heppleston

Table 2. Stepwise results from a backward selection procedure for mixed models with a repeated measures term used to assess the effect of various factors on parental attendance of American Oystercatchers nesting along Bulls Bay or the Atlantic Intracoastal Waterway, Cape Romain Region, South Carolina, USA, May-July 2006. Mixed models conducted separately by location. Number refers to order in which variables were removed (P > 0.10). F statistic and P-values presented for any variables remaining in final model.

	Bulls Bay	Waterway
Brood success	$F_{1,5}$ = 9.4, P = 0.05	$F_{1,16}$ = 6.6, P = 0.02
Nest attempt number	$F_{1,3}$ = 0.06, P = 0.82	5
Brood size	3	6
Chick age	$F_{1,3}$ = 11.2, P = 0.04	4
Chick age^2	2	2
Chick age * brood size	$F_{1,3}$ = 12.2, P = 0.04	3
Chick age^2 * brood size	1	1

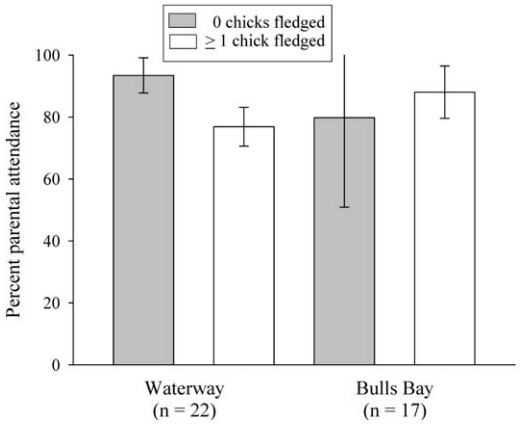

Figure 2. Percent of nest attendance by both parents during the foraging period (weighted mean ± 95% CI) and nest fate of American Oystercatcher pairs in Bulls Bay and along the Atlantic Intracoastal Waterway, Cape Romain Region, South Carolina, USA, May-July 2006. n = number of observation periods. 'Failed nests' fledged 0 chicks, 'Successful nests' fledged ≥1 chick.

1972; Ens *et al.* 1992) leading to an opposing relationship between attendance and reproductive success in the two study groups. Similarly, Nol (1989) found that fledging success of American Oystercatchers in Virginia was positively related to the size of the foraging grounds and the proximity of the foraging grounds to the nesting territory. We suggest that oystercatchers nesting along the Waterway during our study were functioning similarly to leapfrog parents while oystercatchers nesting along Bulls Bay were functioning more similarly to resident parents. Similarly to the aforementioned studies, reproductive success (here measured as DSR during chick-rearing) was lower in the 'leapfrog' study area (i.e. Waterway) compared to the 'resident' study area (i.e. Bulls Bay).

The Eurasian and American oystercatcher systems are not, however, entirely identical with respect to commuter and resident nest territories. For example, breeding sites in our study were discrete, often with one nest per shell rake, and the feeding areas for the commuters and residents also appeared to be distinct (Thibault 2008). In contrast, breeding sites in the aforementioned studies were contiguous, and feeding sites were contiguous with the resident nests. The differences in parental attendance and reproductive success between resident and commuting birds appear to be weaker in our study compared to the Eurasian Oystercatcher studies and this may be due in part to a greater similarity in diet and a more discrete juxtaposition of nesting/foraging sites between our study areas.

Although we postulate that a difference in food availability between the two study areas is the mechanism underlying the opposing relationship we observed between attendance and brood success, alternative hypotheses also merit examination. For example, oystercatchers along the Waterway may have reduced attendance as a means to reduce predation pressure on chicks, subsequently leading to a negative relationship between attendance and brood survival (Skutch 1949). Such behavior should be favored when predation on chicks or eggs increases directly and proximally in relation to parental activity (Martin *et al.* 2000). American and Eurasian oystercatchers have each been shown to reduce attendance at nest sites, especially when disturbance or predation were prevalent (Verhulst *et al.* 2001; McGowan and Simons 2006). However, Verhulst *et al.* (2001) noted that parents reduced attendance in response to current disturbance but not prior events. Therefore, we would expect to observe reduced attendance along the Waterway in response to predation or disturbance only if these occurred during our observation periods, i.e. diurnal, low-tide phases. We observed no signs of diurnal predation on chicks during three years of study in this system (Thibault 2008). Also, attendance rates averaging 80% along the Waterway suggest that parents were not attempting to reduce attendance as a means to distract predators (Sabine *et al.* 2008). In contrast, we did observe adults actively guarding chicks throughout the chick-rearing phase and this is consistent with observations from Safriel (1985) and Sabine *et al.* (2008) who both observed vigilance throughout chick-rearing in Eurasian and American oystercatchers, respectively.

The relationship between attendance rates and brood success may have been affected by differences in diet. However, oystercatchers in Bulls Bay and along the Waterway foraged on the same type and size of

prey items (i.e. intermediate sized oysters; Thibault 2008). Our data do not support the contention that attendance on the Waterway was simply lower due to chick age. In other species of oystercatchers provisioning rates increase and attendance decreases with chick age (Ens *et al.* 1992; Hazlitt *et al.* 2002). Hence, we would have expected parental attendance to be lower in nests from Bulls Bay where chicks were older compared to the Waterway where chicks were younger; such was not the case.

The Cape Romain Region supports the majority of breeding oystercatchers in South Carolina (Sanders *et al.* 2008) and as such plays an important role in the conservation of this declining species in the southeastern U.S. Most of the oystercatchers in this region nest on shell rakes and forage on the shellfish reefs that are interspersed among tidal creeks, bays and the Waterway. Bulls Bay may provide nesting habitat of a slightly higher quality compared to the Waterway with respect to proximity to food resources and parental attendance. Along the Waterway, however, even small intertidal creeks appear to provide foraging sites for oystercatchers. Our data demonstrate that the spatial distribution of food in relation to nest sites may mediate the relationship between parental attendance and brood success. Parents therefore adjust behavior in response to environmental characteristics, and ultimately reproductive success may be affected. As such management of oystercatchers should consider not just direct causes of reproductive failure but also variability in behavioral attributes such as parental attendance in relationship to environmental conditions. In particular, reproductive success should be examined in relation to the juxtaposition of nest sites to foraging areas. Additional research that measures parental and chick behavior during brood-rearing also would enhance our understanding of the trade-off between provisioning and chick-guarding.

ACKNOWLEDGMENTS

We thank M. Spinks, B. Harris, S. Dawsey, M. Connolly, D. Browning and C. Wakefield. This research was funded by the National Fish and Wildlife Foundation (Savannah Santee PeeDee Restoration Fund), a state wildlife grant from the South Carolina Department of Natural Resources, the Department of Forestry of Natural Resources at Clemson University and the USGS South Carolina Cooperative Fish and Wildlife Research Unit. Logistical support was provided by the South Carolina Department of Natural Resources, Cape Romain National Wildlife Refuge and the South Carolina Cooperative Fish and Wildlife Research Unit. K. Schulte assisted with digital orthophotographs of the shellfish reefs and W. Bridges provided statistical assistance. The manuscript benefitted from comments by A. Wilke, W. Bridges, C. McGowan and two anonymous reviewers, 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.

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