NEST-SITE SELECTION OF AMERICAN OYSTERCATCHERS (*HAEMATOPUS PALLIATUS*) IN SALT MARSHES

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ABSTRACT.—We documented flexibility of American Oystercatcher (*Haematopus palliatus*) nest-site selection at marsh habitats in New York, New Jersey, and North Carolina. In New York we examined the relationship of nest-site selection to tidal flooding and found that birds chose nest sites nonrandomly with respect to marshy areas. Three types of habitat patch sites on marsh islands chosen were sand, wrack (tidally washed-up dead organic material), and *Spartina patens* grass. Nests on sandy sites were less susceptible to tidal flooding than nests on wrack or grass because they were higher in elevation. There was a positive correlation between the number of nests and the length of sand beach. Hatching success was higher for eggs placed on sand than for eggs on grass or wrack. The location of sandy nest sites used by birds changed little between years resulting in low turnover rate. Wrack and grass locations changed between years resulting in a high turnover rate.

Birds used different habitats in different geographic areas. In North Carolina, all nests were on sand; none were on wrack or grass. In New York and New Jersey nests were placed on sand, wrack, and grass. Comparisons of nest characteristics showed that sand sites in North Carolina were larger and drier than sand sites in New York and New Jersey. Comparisons between years in New York and New Jersey were different because of the availability of wrack. *Received 22 October 1987, accepted 16 September 1988.*

BIRDS select breeding habitats based on biotic and abiotic factors of the environment. This produces a nonrandom spatial distribution of nests. Breeding-habitat selection can be divided into three categories (Burger 1985): (1) General habitat use involves choice of a broad habitat type such as an oak forest, salt marsh, or prairie; (2) territory acquisition involves selection of an area vigorously defended by one or both members of a pair; and (3) nest-site selection involves the choice of the actual nest location including the substrate on which the nest is placed, cover around the nest, and food availability.

Flexibility in nesting habitat is critical to reproductive success in birds because individuals within populations must adapt to differences in habitat physiognomy. This is particularly true for the American Oystercatcher (*Haematopus palliatus*) because habitat physiognomy changes over the breeding range (Nol 1984), which extends from Massachusetts to Southern Argentina (Hayman et al. 1986). Available descriptions of nesting habitat of the American Oystercatcher (Baird et al. 1884, Bent 1929, Stone 1967) provide no detailed quantitative or comparative examination of habitat selection. The traditional nesting habitat is described as sand dune on barrier island, although recently oystercatchers have nested in marsh habitat (Frohling 1965, Zaradusky 1985). Habitat studies have been conducted on other marsh-nesting species (Beer 1966; Bongiorno 1970; Burger 1974, 1977, 1980; Burger and Lesser 1978; Montevecchi 1978; Howe 1982), but we know of no comparisons of a salt-marsh nesting species in different geographical regions.

Oystercatchers generally nest in open habitats that are sparsely vegetated (Webster 1941, Legg 1954, Harris 1967, Heppleston 1972, Hartwick 1974, Martinez et al. 1983, Summers and Cooper 1977). Most species nest near the shoreline, but European Oystercatchers (*Haematopus ostralegus*) and Magellanic Oystercatchers (*Haematopus leucopodus*) also nest in inland habitats (Baker 1973, Buxton 1961, Falla et al. 1966, Heppleston 1972, Miller and Baker 1980). Thus, some species are flexible in choice of nesting habitat. Another indication of flexibility in nesting-habitat selection is the recent range expansion of American Oystercatchers (Post 1960, Post and Rayner 1964, Zaradusky 1985), American Black

The Auk 106: 185-192. April 1989

Oystercatchers (*Haematopus bachmani*; Eley 1976), and European Oystercatchers (Buxton 1961, Dobbs 1970).

STUDY AREA AND METHODS

We observed 31 nests (1983) and 59 nests (1984) in New York at Great South Bay and South Oyster Bay (40°37'N, 73°24'W) between the Wantagh State Parkway and Oak Beach. Ninety-one marsh islands lay between the Jones Beach barrier island and Long Island. The islands ranged in size from <1 ha to 844 ha; the median was 40.58 ha. We defined a marsh island as an area surrounded by 30-cm-deep water at low tide and not connected to either Long Island or the barrier island. We chose 30 cm because young chicks were unable to walk to nearby islands at this depth. The dominant species of vegetation in the study area were *Spartina alternaflora* and *S. patens.*

In 1984, we examined 19 nests in Barnegat Bay, New Jersey (39°45'N, 78°08'W). Barnegat Bay contains 259 salt-marsh islands between the barrier island and the mainland. The predominate species of vegetation were *S. alternaflora* and *S. patens* in the wetter areas with *Iva frutescens* and *Baccharis halimifolia* in drier areas (Burger and Lesser 1978).

In 1984, we examined 18 nests at Battery Island, North Carolina (33°54'N, 78°01'W), a natural island with deposits of dredged material. It was dominated by a dense grass community of primarily *S. patens* and a maritime shrub thicket dominated by *Xanthoxylum americanum, Ilex vomitoria, Quercus virginiana, Juniperus virgiana, Myrica cerifera, B. halimifolia* and *I. frutescens* (Parnell and Soots 1979).

In New York we collected data for each nest site to examine habitat-use flexibility and adaptations to marsh habitats. We defined a nest site as the nest scrape and the surrounding habitat patch. A habitat patch is classified by its substrate of sand, wrack, or *S. patens* grass (see Fig. 1). Sand patches are created when dredged spoil is deposited on the marsh. Wrack patches consist of dead organic material that washes up on the marsh during tidal flooding. Grass patches are on naturally high regions covered by *S. patens,* easily distinguished from *S. alternaflora* areas. Sandy patches are higher in elevation and less susceptible to flooding than wrack and grass patches. Low sites were those in which nests were placed on grass and wrack substrate; high sites were those in which nests were placed on sand substrate.

In New York we used a measuring wheel to survey the dimensions of all high sites. The area of all sites was calculated from these measurements to determine if there was a difference in frequency of nest sites on the barrier island compared to marsh islands, and if there was a correlation between the length of sand beach and number of nests. We used length for the correlation calculation because most sandy sites were long but not very wide. We censused only the bay side of the barrier island.

We calculated turnover rate (after Erwin et al. 1981) to examine the stability of nest sites from year to year. Nest sites from 1983 were surveyed in 1984 to note if sites had changed. We noted new sites in 1984. The turnover rate is

$$T = \frac{1}{2}\left(\frac{S_1}{N_1} + \frac{S_2}{N_2}\right),$$

where S_1 is the number of sites occupied only on the first census, N_1 is the total number of sites occupied on the first census, S_2 is the number of sites occupied only on the second census, and N_2 is the total number of sites occupied on the second census.

We collected the following data for nest sites and randomly chosen sites on islands: the percentage of vegetation, sand, and wrack within 1-m and 5-m radii around the nest, width and length of nest sites and distance to water (creek or bay). A random point for each nest was chosen from a grid system of each nesting island. Measures of these nest-site characters yielded information on the degree of protection provided from tidal flooding. We also compared years using the same nest characters. All comparisons were made using Kruskal-Wallis Chi-square tests rather than analysis of variance because the data were not distributed normally.

We measured nest-site elevation on the sandy dredge-spoil area of North Line Island (40°38'N, 73°29'W) because we assumed competition for sites to be great due to the high concentration of breeding pairs (9 in 1983; 14 in 1984). We used a Nixon level accurate to 0.03 m to measure elevation (above sea level) with respect to survey markers.

We collected data on hatching success in New York in 1983 and 1984. A nest was considered successful if at least one chick hatched. We did not determine fledgling success because the parents led the chicks away from the nest after hatching.

We examined geographic variation in nest-site selection between New York, New Jersey, and North Carolina by comparing the percentage of vegetation, sand, and wrack within 1-m and 5-m radii around the nest, length and width of the nest site, and distance to water.

RESULTS

Adaptations to marsh nesting in New York.—The number of nests on high sites on marsh islands was significantly greater with respect to available sand than the number of nests on high sites on barrier islands in 1983 and 1984 (1983: $\chi^2 = 21.6$, df = 1, $P < 0.005$; 1984: $\chi^2 = 56.4$, df = 1, $P < 0.005$). There was no relationship be-

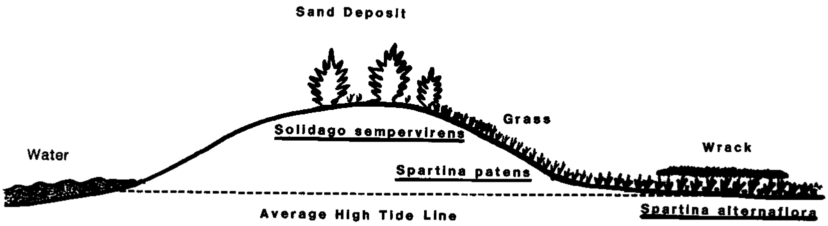

Fig. 1. Profile of marsh island habitat, illustrating the differences in elevation of the three basic types of nest-site locations: sand, grass, and wrack.

tween number of nests and island size but there was a positive correlation for number of nests and length of sandy areas (1983: $r = 0.69$, $P < 0.06$; 1984: $r = 0.69$, $P < 0.006$).

We compared nest-site types (high and low) for frequency of occurrence, turnover rate, and hatching success to determine if there was a relationship between habitat type and reproductive success. In both years more birds nested on high sites than low sites (Table 1). All of the high sites used in 1983 were used again in 1984. The turnover rate between years was 0.24 because of the increased use of habitat as a result of a population increase.

Thirty-five percent of low sites used in 1983 were used again in 1984. The turnover rate was 0.74 and was related to wrack availability. In 1983, 78% of low nests were on wrack, but in 1984 the amount of wrack decreased and all nests were on *S. patens* (Table 1). In 1983, young hatched in only 22% of low nests; in 1984, hatch occurred in 43%. Young hatched in 60% (1983) and 64% (1984) of high nests. Therefore nests placed on high sites were more stable in location between years and had a higher reproductive success than nests placed on low sites.

We compared high and low nest sites to random sites and found that in 1983 all measured characteristics differed significantly (Tables 2, 3). All random sites were grass areas while nest sites were mainly on wrack or sand. Nest sites had greater amounts of sand and wrack, and smaller amounts of live vegetation, in comparison to random sites. Accordingly, width and length of wrack and sand areas were greater than those of random sites. Nest sites were farther away from a water body than random sites.

In 1984, high sand nesting-site patterns were similar to 1983. Low nesting sites had a different pattern, however, and were mainly on grass and not wrack (Tables 1, 3). Between years, 57% of nest characters were significantly different for low sites, but only 17% of characters were different for high sites (Table 4).

On North Line Island, nests in 1983 were 1.08 ± 0.41 m above sea level and nests in 1984 were 1.01 ± 0.18 m above sea level; random points were 0.69 ± 0.33 and 0.58 ± 0.29 m above sea level in 1983 and 1984, respectively. In both years nests were significantly higher than random points (1983: $\chi^2 = 8.76$, df = 1, $P < 0.003$; 1984: $\chi^2 = 6.83$, df = 1, $P < 0.01$). Thus, oystercatchers selected areas least susceptible to tidal flooding.

Geographic variability.—In North Carolina all nests were on high sites (Table 1) while in New Jersey only 58% of nests were on high sites. In New Jersey, 50% of low sites were on wrack, and 50% were on grass. In New York (1983 and 1984), birds nested on high and low sites (see previous section for details).

High sandy sites in North Carolina were larger and drier than nesting sites in New York and New Jersey (Tables 2, 5). In North Carolina most nest characteristics were significantly greater than New York in 1983 and 1984 (Tables 2, 5). However, the North Carolina and New York 1983 values for the amount of sand and vegetation within a 5-m radius of the nest were not significantly different. In New York in 1983 the population was smaller than in 1984 (Table 1) and therefore larger, sandier areas were used.

TABLE 1. Frequency of nest sites.

		High	Low	
	Total	Sand	Wrack	Grass
New York 1983	31	22	7	2
New York 1984	59	52	0	7
New Jersey 1984	19	11	4	4
North Carolina 1984	18	18	0	0

TABLE 2. Means and standard deviations of nest characteristics for high and low nesting sites in New York, New Jersey, and North Carolina. Random sites (on islands) were chosen using a table of random numbers.

	New York 1983			
	High sites		Low sites	
Characteristics	Nest	Random	Nest	Random
% Wrack or sand/1-m circle	57.91 ± 29.65	18.52 ± 25.98	75.90 ± 27.41	12.00 ± 28.98
% Vegetation/1-m circle	44.19 ± 31.95	77.95 ± 31.73	24.10 ± 7.41	87.70 ± 28.85
% Wrack or sand/5-m circle	56.00 ± 29.54	19.42 ± 23.04	59.20 ± 31.67	17.90 ± 12.41
% Vegetation/5-m circle	41.71 ± 27.23	77.14 ± 25.19	41.70 ± 32.46	74.20 ± 23.75
Distance to water (m)	7.59 ± 3.49	2.33 ± 3.28	23.04 ± 11.38	3.90 ± 4.42
Habitat patch width (m)	7.39 ± 3.54	0.53 ± 0.96	6.63 ± 4.02	0.40 ± 0.70
Habitat patch length (m)	113.75 ± 139.80	1.99 ± 3.78	22.69 ± 26.09	1.38 ± 3.14

In 1983 New York sites were similar to North Carolina. In North Carolina the amount of sand was not significantly different from New Jersey. The distance to water, the length, and the width of nest sites were significantly greater in North Carolina than in New Jersey and New York in 1983 and 1984. The percentage of vegetation and sand, the length and width of nest site, and the distance to water were not significantly different for high sites in New Jersey and New York in 1983 and 1984. One exception was that the percentage of sand within a 1-m radius of the nest was greater in New Jersey than in New York in 1984.

We compared low nesting sites only between New Jersey and New York because North Carolina had no low nests. The length and width of marsh wrack were greater in New Jersey than in New York in both years. In 1984, this effect was particularly pronounced in New York because all low-lying nests were on grass and none was on wrack. The lack of nests on wrack in New York in 1984 also explains why the New Jersey values were significantly different in the amount of wrack and vegetation.

DISCUSSION

Flexibility in nesting-habitat choice is important to the success of a species that breeds over a large geographic region because of the biological constraints of food availability, predation, and competition. Abiotic limitations of the physical environment (such as weather, available space, and physiognomy of habitat) also play a critical role in flexibility. Flexibility in nest-site choice can minimize the costs of tidal flooding or predation, thereby increasing reproductive success. This may result in higher population numbers and expansion into new habitats.

Adaptations to marsh nesting.—In New York more birds nested on marsh islands than barrier islands, perhaps because of increased human use of the barrier island and lower predation rates on marshes. Similarly, breeding areas of African Black Oystercatchers (*Haematopus moquini*) are threatened by human use of beaches (Summers and Cooper 1977, Hockey 1983). Several colonial birds which nested only on barrier islands presently nest on barrier and marsh is-

TABLE 2. Continued.

	New York 1984			
	High sites		Low sites	
Characteristics	Nest	Random	Nest	Random
% Wrack or sand/1-m circle	48.10 ± 30.55	11.15 ± 20.11	4.00 ± 10.58	21.43 ± 27.80
% Vegetation/1-m circle	50.62 ± 30.40	84.75 ± 25.56	99.71 ± 0.95	79.00 ± 27.76
% Wrack or sand/5-m circle	40.56 ± 24.12	11.62 ± 16.31	4.57 ± 7.72	25.00 ± 30.14
% Vegetation/5-m circle	54.39 ± 20.50	82.79 ± 25.69	94.00 ± 11.65	74.29 ± 28.94
Distance to water (m)	12.74 ± 14.43	5.91 ± 9.30	26.34 ± 22.07	3.53 ± 4.52
Habitat patch width (m)	10.26 ± 13.91	0.29 ± 0.53	0.30 ± 0.79	0.46 ± 0.93
Habitat patch length (m)	77.16 ± 107.08	0.00 ± 1.65	0.59 ± 1.55	0.54 ± 1.04

TABLE 2. Continued.

Characteristics	New Jersey 1984 High sites Nest	New Jersey 1984 Low sites Nest	N. Carolina 1984 High sites Nest
% Wrack or sand/1-m circle	67.92 ± 33.33	69.17 ± 18.00	79.28 ± 16.20
% Vegetation/1-m circle	29.85 ± 31.01	30.50 ± 18.38	23.61 ± 23.75
% Wrack or sand/5-m circle	42.23 ± 38.73	37.00 ± 40.59	67.11 ± 22.56
% Vegetation/5-m circle	51.46 ± 37.55	59.50 ± 39.07	27.94 ± 16.89
Distance to water (m)	10.06 ± 6.94	18.73 ± 7.12	21.45 ± 8.98
Habitat patch width (m)	9.59 ± 10.06	13.65 ± 5.80	33.00 ± 15.39
Habitat patch length (m)	47.72 ± 53.09	74.98 ± 27.99	339.44 ± 295.52

lands, a difference attributed to increased human use of beaches (Burger 1980, Erwin 1980, Rodgers and Burger 1981). Predation on barrier islands from mammalian predators such as raccoons (*Procyon lotor*), foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) may influence breeding birds to move onto marsh habitats (Krunk 1964, Summers and Cooper 1977, Greenwood 1982, Moller 1983, Pierce 1986). In New York predation on marsh islands seemed to be low. Predation by a rat (*Rattus* sp.) and by a gull (*Larus* sp.) were noted only once.

Oystercatchers nonrandomly chose nest sites with respect to physiognomic features of the marsh. Nest sites were generally patches of sand or wrack which had more substrate and less vegetation, and they were farther from a water body (creek or bay) than randomly selected sites on nesting islands. On North Line Island, sand nest sites were higher in elevation than randomly chosen sites around the breeding area. Nesting at higher elevation is critical to marsh-breeding birds because nests can be destroyed by tidal flooding. Therefore, sand nests should flood less and have a higher success rate, as we found. We suggest that sand nests are selected more frequently and have a lower turnover rate because they were more successful. Several other marsh-nesting species exposed to tidal flooding nest on high sandy sites on marsh islands. Herring Gulls (*Larus argentatus*) and Willets (*Catoptrophorus semipalmatus*) are two examples (Burger 1980, Howe 1982).

Low nests had lower hatching success compared to high nests, but they showed moderate success. Thus, it is advantageous to nest on wrack and grass when sand sites are limited. The advantages to nesting on wrack are that it floats to provide a raft for nests, it is higher in elevation than the surrounding area, and it is farther from water than sand nests and random sites. Conversely, wrack is lower in elevation than sand locations and its availability and location varies between years which results in high turnover rates. The few grass nests were in high areas covered with *S. patens* that provided refuge from tidal flooding.

Geographical comparisons.—American Oystercatchers breed in two types of general habitat on the east coast of the United States: sand dunes

TABLE 3. Comparison of nest sites and random sites in New York for different nest characteristics.

Characteristics	1983 High sites χ^2	1983 High sites P	1983 Low sites χ^2	1983 Low sites P	1984 High sites χ^2	1984 High sites P	1984 Low sites χ^2	1984 Low sites P
% Wrack or sand/1-m circle	14.04	0.0002	11.29	0.0008	40.70	0.0001	2.45	NS
% Vegetation/1-m circle	8.57	0.0034	10.77	0.0010	29.86	0.0001	6.83	0.0090
% Wrack or sand/5-m circle	15.86	0.0001	8.70	0.0032	36.62	0.0001	1.35	NS
% Vegetation/5-m circle	14.40	0.0001	4.49	0.0340	35.11	0.0001	3.49	NS
Distance to water (m)	17.57	0.0001	11.59	0.0007	24.01	0.0001	5.61	0.0178
Habitat island width (m)	29.30	0.0001	11.54	0.0007	74.40	0.0001	1.08	NS
Habitat island length (m)	27.19	0.0001	11.03	0.0009	70.62	0.0001	0.77	NS

TABLE 4. Comparison of years 1983 and 1984 in New York for nest characteristics.

	High sites		Low sites	
Characteristics	χ^2	P	χ^2	P
% Wrack or sand/1-m circle	1.48	NS	9.18	0.0072
% Vegetation/1-m circle	1.11	NS	8.61	0.0037
% Wrack or sand/5-m circle	4.54	0.0336	10.17	0.0016
% Vegetation/5-m circle	2.96	NS	7.95	0.0048
Distance to water (m)	3.10	NS	0.12	NS
Habitat island width (m)	0.24	NS	0.40	NS
Habitat island length (m)	0.11	NS	0.01	NS

along barrier islands (Bent 1929, Nol 1984) and salt-marsh islands (Zaradusky 1985, this study). In New York, birds rarely nested in sand dune habitats. In North Carolina and New Jersey oystercatchers commonly nest in sand dune habitats (Bent 1929, Parnell pers. comm., pers. obs.).

Choice of marsh-nesting habitat by the American Oystercatcher was flexible geographically. In North Carolina all nests were on sparsely vegetated sand habitat. High sand nest sites in North Carolina had more sand, were wider and longer, and were farther from the water than in New York and New Jersey. Nests were on elevated, drier habitat. In North Carolina oystercatchers nested on sparsely vegetated sand areas (Soots and Parnell, 1975). Parnell (pers. comm.) noted that oystercatchers did not nest directly on marsh wrack or grass in this area.

In New York and New Jersey oystercatchers nested on all three types of habitat: the most common was sand, followed by marsh wrack and *Spartina* grass. The birds nesting on marsh islands in New York and New Jersey used habitat differently than in North Carolina. Although nest characters differed in all locations, oystercatchers nested at higher elevations than the surrounding area and on loose substrate such as wrack and sand.

The importance of flexibility to re-expansion.—When nesting habitat is limited, birds can forego breeding, adapt to new habitats, expand into similar habitats elsewhere, or they can adapt to a new habitat in other areas. Flexibility is an important aspect of adapting to new environments during a range expansion.

In the past 20 years, oystercatchers have re-expanded north into New Jersey, New York, and Massachusetts (Post 1960, Post and Raynor 1964, Zaradusky 1985). This may have been possible in part because of the adaptation to marsh nesting. Oystercatchers were reported nesting on marshes in New Jersey in 1965 (Frohling 1965). Frohling suggested that marsh nesting may be an important adaptation to oystercatcher populations because human beach use decreased available nesting areas and forced birds to nest in other habitats. Our data support his suggestion. Thus, nesting on sand, as well as wrack and grass on marsh islands, may be an important aspect of the expansion and resulting increase in oystercatcher populations in the Northeast.

TABLE 5. Comparisons of nest characteristics between New York (NY), New Jersey (NJ), and North Carolina (NC) for high and low sites.

	NY 1983 vs. NJ 1984				NY 1984 vs. NJ 1984			
	High sites		Low sites		High sites		Low sites	
Characteristics	χ^2	P	χ^2	P	χ^2	P	χ^2	P
% Wrack or sand/1-m circle	1.63	NS	1.19	NS	4.94	0.0262	9.99	0.0016
% Vegetation/1-m circle	2.38	NS	1.18	NS	5.35	0.0207	9.25	0.00234
% Wrack or sand/5-m circle	2.07	NS	1.43	NS	0.01	NS	0.87	NS
% Vegetation/5-m circle	0.72	NS	0.85	NS	0.01	NS	3.28	NS
Distance to water	0.01	NS	0.05	NS	0.56	NS	0.18	NS
Habitat island width (m)	0.02	NS	5.20	0.0225	0.23	NS	10.02	0.0015
Habitat island length (m)	1.67	NS	6.53	0.0106	0.62	NS	9.99	0.0016

ACKNOWLEDGMENTS

Special thanks to John Zaradusky and Mark Shields for their assistance in locating nest sites and for providing useful field information. We are grateful to Anthony J. Lauro for his assistance in the collection of elevation data. Finally, we appreciate comments on the manuscript from Erica Nol and William Boarman. This project was funded by the Leathem-Steinetz fund of Rutgers University.

LITERATURE CITED

BAKER, A. J. 1973. Distribution and numbers of New Zealand oystercatchers. Notornis 20: 128-144.

BAIRD, S. F., T. M. BREWER, & R. RIDGEWAY. 1884. The waterbirds of North America, vol. 1. Boston, Little, Brown and Co.

BEER, C. G. 1966. Adaptations of nesting habitat in the reproductive behaviour of the Black-billed Gull *Larus bulleri*. Ibis 108: 392-410.

BENT, A. C. 1929. Life histories of North American shorebirds, part 2. U.S. Natl. Mus. Bull. 146.

BONGIORNO, S. F. 1970. Nest site selection by adult Laughing Gulls (*Larus atricilla*). Anim. Behav. 18: 434-444.

BURGER, J. 1974. Breeding adaptations of Franklin's Gull (*Larus pipixcan*) to a marsh habitat. Anim. Behav. 22: 521-567.

———. 1977. Nesting behaviour of Herring Gulls: invasion into *Spartina* salt marsh areas of New Jersey. Condor 79: 162-169.

———. 1980. Nesting adaptation of Herring Gull (*Larus argentatus*) to salt marshes and storm tides. Biol. Behav. 5: 147-162.

———. 1985. Habitat selection in temperate marsh-nesting birds. Pp. 253-281 *in* Habitat selection in birds (M. Cody, Ed.). London, Academic Press.

———, & F. LESSER. 1978. Selection of colony sites and nest sites by Common Terns (*Sterna hirundo*) in Ocean County, New Jersey. Ibis 120: 433-449.

BUXTON, E. J. 1961. The inland breeding of the oystercatcher in Great Britain, 1958-1959. Bird Study 8: 194-209.

TABLE 5. Extended.

NY 1983 vs. NC		NY 1984 vs. NC		NJ vs. NC	
High sites		High sites		High sites	
χ^2	P	χ^2	P	χ^2	P
5.17	0.0230	15.43	0.0001	0.25	NS
0.37	0.0380	12.04	0.0005	0.07	NS
1.12	NS	13.58	0.0002	2.38	NS
2.19	NS	17.82	0.0001	1.75	NS
24.07	0.0001	16.72	0.0001	6.39	0.0105
28.07	0.0001	36.43	0.0001	16.78	0.0001
9.87	0.0017	18.97	0.0001	14.75	0.0001

DOBBS, A. 1970. Extension of the breeding range of the oystercatcher to the midlands. British Birds 63: 428.

ELEY, T. J., JR. 1976. Extension of the breeding range of the Black Oystercatcher in Alaska. Condor 78: 115.

ERWIN, R. M. 1980. Breeding habitat use by colonially nesting waterbirds in two mid-Atlantic U.S. regions under different regimes of human disturbance. Biol. Conserv. 18: 39-51.

———, J. GALLI, & J. BURGER. 1981. Colony site dynamics and habitat use in Atlantic coast seabirds. Auk 98: 550-561.

FALLA, R. A., R. B. SIBSON, & E. G. TURBOTT. 1966. A field guide to the birds of New Zealand and outlying islands. London, Collins.

FROHLING, R. C. 1965. American Oystercatcher and Black Skimmer nesting on salt marsh. Wilson Bull. 77: 193-194.

GREENWOOD, R. J. 1982. Nocturnal activity and foraging of prairie raccoons (*Procyon lotor*) in North Dakota. Am. Midl. Nat. 107: 238-243.

HARRIS, M. P. 1967. The biology of Oystercatchers (*Haematopus ostralegus*) on Skokholm Island, S. Wales. Ibis 109: 180-193.

HARTWICK, E. B. 1974. Breeding ecology of the Black Oystercatcher (*Haematopus bachmani* Audubon). Syesis 7: 83-92.

HAYMAN, P., J. MARCHANT, & T. PRATER. 1986. Shorebird: an identification guide to the waders of the world. Boston, Houghton Mifflin Co.

HEPPLESTON, P. B. 1972. The comparative breeding ecology of Oystercatchers (*Haematopus ostralegus*) in inland and coastal habitats. J. Anim. Ecol. 4: 23-51.

HOCKEY, P. A. R. 1983. The distribution, population size, movements, and conservation of the African Black Oystercatcher (*Haematopus moquini*). Biol. Conserv. 25: 233-262.

HOWE, M. A. 1982. Social organization in a nesting population of Eastern Willets (*Catoptrophorus semipalmatus*). Auk 99: 88-102.

KRUNK, A. 1964. Predator and anti-predator behavior of the Black-headed Gull (*Larus ridibundus*). Behav. Suppl. 11: 1-29.

LEGG, K. 1954. Nesting and feeding of the Black Oystercatcher near Monterey, California. Condor 56: 359-360.

MARTINEZ, A., A. MOTIS, E. MATHEU, & F. LLIMONA. 1983. Data on the breeding biology of Oystercatchers (*Haematopus ostralegus*) in the Ebro Delta. Ardea 71: 229-234.

MILLER, E. H., & A. J. BAKER. 1980. Displays of the Magellanic Oystercatcher (*Haematopus leucopodus*). Wilson Bull. 92: 149-168.

MOLLER, A. P. 1983. Damage by rats (*Rattus norvegicus*) to breeding birds on Danish Islands. Biol. Conserv. 25: 5-18.

MONTEVECCHI, W. A. 1978. Nest site selection and its survival value among Laughing Gulls. Behav. Ecol. Sociobiol. 4: 143-161.

NOL, E. 1984. Reproductive strategies in the Oystercatcher (Aves: Haematopodidae). Ph.D. dissertation, Toronto, Univ. Toronto.

PARNELL, J. F., & R. F. SOOTS JR. 1979. Atlas of colonial waterbirds of North Carolina estuaries. UNC Sea Grant Prog. Publ., UNC-SG-78-10.

PIERCE, R. 1986. Differences in susceptibility to predation during nesting between Pied and Black stilts (*Himantopus* spp.). Auk 103: 273-280.

POST, P. 1960. The American Oystercatcher in New York. Kingbird 11: 3-6.

POST, P. W., & G. S. RAYNOR. 1964. Recent range expansion of the American Oystercatcher into New York. Wilson Bull. 76: 339-346.

RODGERS, J. A., & J. BURGER. 1981. Concluding remarks: symposium on human disturbance and colonial waterbirds. Colonial Waterbird 4: 69-70.

SOOTS, R. F., JR., & J. F. PARNELL. 1975. Ecological succession of breeding birds in relation to plant succession on dredge islands in North Carolina estuaries. UNC Sea Grant Prog. Publ., UNC-SG-715-27.

STONE, W. 1967. Bird studies at Old Cape May: an ornithology of coastal New Jersey, vol. 1. New York, Dover.

SUMMERS, R. W., & J. COOPER. 1977. The population, ecology and conservation of the Black Oystercatcher (*Haematopus moquini*). Ostrich 48: 28-40.

WEBSTER, J. D. 1941. The breeding of the Black Oystercatcher. Wilson Bull. 53: 141-156.

ZARADUSKY, J. D. 1985. Breeding status of the American Oystercatcher in the town of Hempstead. Kingbird 35: 105-113.