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NEST-SITE AND COLONY CHARACTERISTICS OF WADING BIRDS IN SELECTED ATLANTIC COAST COLONIES

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Along the Atlantic Coast colonies of herons, egrets and ibises nest in diverse habitats ranging from small shrubs to tall trees (Bent 1926, Custer and Osborn 1977). Often colonies occur where there appear to be large amounts of similar, unused habitat (Bent 1926, Jenni 1969, McCrimmon 1978) suggesting that social factors predominate in the selection of a colony site (see Krebs 1974, for review).

The role of social factors in the dispersion of species and their nests within a colony is not so well known. Usually nests of the same species are built in a variety of sites in colonies with differing vegetation. Several authors have provided qualitative assessments of nesting sites (Eyles 1938, Gersbacher 1939, Patten 1952, Meanley 1955, Ralph and Ralph 1958, Dusi 1966, Lowe-McConnell 1967, Dusi and Dusi 1968, Maxwell and Kale 1977), but it seems clear that their descriptions apply to the specific colony sites where they worked, and considerable variation exists between studies.

Within a colony, nests of various species are not easily differentiated, even by experienced observers (Bent 1926, pers. obs.). However, quantitative methods and detailed behavioral observations suggest that slight, but significant differences in nest-site characteristics do exist. Jenni (1969) and Maxwell and Kale (1977) reported differences in vertical and horizontal placement by wading birds in a Florida heronry. Burger (1978) noted similar patterns in a number of heronries on the Atlantic Coast and in tropical areas. Using multivariate statistical analyses of nest-site variables, McCrimmon (1978) demonstrated a fine vertical and horizontal separation in a heronry in North Carolina. Burger (1978) has inferred the mechanism of nest-site separation is dominance; larger species nest higher in the vegetation than subordinate smaller ones.

These observations suggest that both social and vegetation factors influence the placement of the nest. This paper examines characteristics of nest placement and dispersion in relation to vegetation in the colony. Social interactions were not directly examined, but we discuss their possible role in spacing of nests and choice of nesting sites. Six colonies and 5 species were examined in detail. This project was a part of a larger study of the value of herons and their allies as indicators of the environmental conditions in Atlantic coast estuaries (Custer and Osborn 1977).

COLONY LOCATION AND DESCRIPTION

Study sites were selected from the heron colonies located earlier in the year where nests had been marked for demographic investigation (Custer and Osborn 1977). Colonies on Spectacle and Clark's islands, Massachusetts, 2 colonies in Swash Bay, Virginia, and 2 colonies in Middle Marsh, North Carolina, were chosen because they represent various combinations of heron species and vegetation types (Table 1).

Spectacle Island (42°19.5'N, 70°59.2'W) was formerly the site of the Boston city dump. The center of the island is filled with compacted trash. The edges drop steeply into the bay from a height of 20 m. Herons nest mostly in small, closely spaced apple (*Pyrus malus*), cherry (*Prunus* spp.), buckthorn (*Rhamnus* spp.), poplar (*Populus heterophylla*) and sumac (*Rhus typhina*) trees (5–6 m in height). Where trees are dense there is little ground vegetation and much of the soil contains broken glass and rusting pieces of metal.

Clark's Island (42°0.7'N, 70°38.2'W, elev. 10 m) is thickly covered with shrubs and trees. Common types of vegetation (2–5 m) used by nesting herons include arrow wood (*Viburnum* spp.), high bush blueberry (*Vaccinium corymbosum*), shad bush (*Amelanchier* spp.) and juniper (*Juniperus* spp.). One side of the island is inhabited, but apparently there is very little disturbance to nesting herons.

The 2 Swash Bay colonies (37°32.0'N, 75°40.5'W) are located on a large sand flat island of a dredge spoil (elev. 1 m). We named these colonies south-south west (SSW) and north-north east (NNE) according to their positions. The vegetation is still in an early stage of succession, probably because of the continuous dumping of spoils on the island. Highwater shrub (*Iva frutescens*) is the dominant plant on both islands.

Middle Marsh colonies (elev. 1 m) are located on 2 islands in a large estuary near Beaufort, North Carolina. A survey marker dated 1933 was found on Middle Marsh Island (34°41.6'N, 76°36.9'W) suggesting it is at least 42 years old. Vegetation is mostly a dense growth of shrub and small trees (1–5 m) of yaupon (*Ilex vomitoria*), live oak (*Quercus virginiana*), highwater shrub and poison ivy (*Rhus radicans*). The Lower Middle Marsh colony (34°41.3'N, 76°36.8'W), 0.5 km southwest of the Middle Marsh colony, is much smaller than the more northern colony.

METHODS AND MATERIALS

The site characteristics of each nest, its position relative to other nests, and vegetative patterns within the colony were quantified. Eleven characteristics of nest-sites were measured (Table 2). The set of measurements reflects nest-site conditions that were mostly independent of the seasonal growth of the vegetation. The variables OPEN and EXIT are the weakest in this regard. Four (GRD, TOP, CTR, OUT) are related to the vertical and horizontal location of the nest in the supporting vegetation. Two represent measures of nest stability (DEF) and exposure (OPEN). Other information included the time of nest initiation (TIM), nest success (SUC), the probable direction of entrance into, or exit from, the nest (EXIT), species (PSP) and condition (PCON) of the vegetation which supported the nest. These last 3 variables were used in the study of nest dispersion and colony characteristics, but not the analysis of nest-site characters. This was because no suitable transformation of radial measures (EXIT) was available in the statistical package and because plant species (PSP) is a nominal variable which yields no useful numerical result. PCON was omitted because it could not be consistently applied in all colonies.

Variables were measured in metric units or converted to metric units before analysis. GRD, TOP and CTR were transformed ($\log_e$) to product homogeneous variances and to reduce skewness and kurtosis.

The variable set was subjected to a factor analysis (subprogram FACTOR, SPSS, Nie et

TABLE 1
SUMMARY OF COLONIES STUDIED, THEIR SPECIES COMPOSITION AND ABUNDANCE AND INVESTIGATORS INVOLVED WITH MARKING NESTS

Colony	Species[b]	Number of nests[a] Active	Measured[c]	Investigator
Spectacle Island,	SNEG	66	47	J. J. Hatch
Massachusetts	BNHE	161	43	Dept. Biology
	GLIB	5	—	Univ. Massachusetts, Harbor
				Campus, Boston, Massachusetts
Clark's Island,	GREG	5	—	B. A. Harrington
Massachusetts	SNEG	150	34	Manomet Bird Observatory
	LBHE	5	—	Manomet, Massachusetts
	BNHE	350	30	
	GLIB	45	21	
	CAEG	3	—	
			SSW/NNE	
Swash Bay,	GREG	1	—	M. A. Byrd, T. F. Wieboldt
Virginia[d]	SNEG	150	51/103	and J. W. Bill Akers
	LOHE	180	18/23	Dept. Biology
	LBHE	2	—	Coll. of William and Mary
	GLIB	8	0/8	Williamsburg, Virginia
Middle Marsh,	GREG	44	53	J. O. Fussell, III
North Carolina	SNEG	29	11	Box 520
	LOHE	10	8	Morehead City, North Carolina
	BNHE	7	8	
Lower Middle Marsh,	GREG	23	28	J. O. Fussell, III
North Carolina	SNEG	24	30	
	LOHE	49	55	
	LBHE	16	17	
	BNHE	2	—	
	GLIB	5	—	
	CAEG	1	—	

[a] Estimate of nests represents the maximum number active at any 1 time (see Osborn and Custer 1978). The number of nests measured may exceed the estimated number because of this.
[b] Species abbreviations are: GREG—Great Egret; SNEG—Snowy Egret; LOHE—Louisiana Heron; LBHE—Little Blue Heron; BNHE—Black-crowned Night Heron; GLIB—Glossy Ibis; CAEG—Cattle Egret.
[c] Measured by us.
[d] Information for 3 Swash Bay colonies are combined; we were able to measure nests in only 2 colonies.

al. 1970). The procedure produces a correlation matrix among the measured variables which is then used to create linear combinations of the original variables called factors (or principal components), that are uncorrelated with each other (orthogonal). These factors account for all of the variation in the original data. The number of factors produced by the procedure is equal to the number of variables in the original data set. However, usually the first few factors explain a very large proportion of the total variation in the data. Herein rests the

TABLE 2

LIST OF VARIABLES MEASURED TO DESCRIBE THE NEST-SITES OF WADING BIRDS

Measurements	Description
GRD (nest height)	distance from the ground to the top edge of the nest
TOP (height above the nest)	distance from the top of the nest to the top of the vegetation (in an imaginary 15 cm diameter cylinder projected vertically above the nest)
CTR (distance to center)	distance from the center of the nest to the center(s) of the main supporting structures (measured from the nest to a vertically projected line in the center of the supporting structure)
OUT (distance to the outside)	distance from the center of the nest to the outside of the supporting structure on the axis through the nest and support center (in an imaginary 15 cm diameter cylinder projected horizontally from the nest)
DEF (nest deflection)	amount of displacement vertically when a standard 1200 g weight was placed in the nest (geometric scale)
OPEN (nest angle)	the degree of exposure of the nest to the sky, measured by compass as the arc of a circle to the nearest 10°
EXIT[a] (nest opening)	the probable direction of entrance and exit used by the nesting bird, measured as the compass bearing to the nearest 10°
TIM (month eggs laid)	categories: March, April, May, June, July
SUC (reproductive success of nest)	categories: never active, eggs laid but not hatched, and eggs hatched
PSP[b] (support species)	species of plant(s) supporting the nest
PCON[b] (condition of support)	categories: dead, live, partially dead

[a] This variable was used only in relation to nest dispersion.
[b] Nominal variables were not used in the multivariate analysis.

power of factor analysis where a large set of variables can potentially be reduced to a manageable few. A further refinement of the factors can be obtained by rotation in matrix space. This produces a better fit to the data for the derived factors (see Nie et al. 1970 for a graphical treatment). We used the option VARIMAX rotation in the SPSS package to emphasize the difference between factors.

Factors by themselves do not reveal nest-site patterns for individual species of wading birds. For this analysis, which is of interest because of possible resource division, a procedure was used to calculate a mean factor score (or mean vector) for each species of bird along each factor (FACSCORE procedure in SPSS package). It was then possible to view each species' position on every factor generated in the analysis of the data.

We also examined the extent to which physical characteristics of nesting sites were correlated with time of nest initiation and nesting success. Canonical correlation, which is akin to regression, but more general, was used to answer this question. By this technique pairs of factors are extracted simultaneously from a variable matrix composed of an independent variable set (in this case vegetation characters) and a dependent set (time and success) (Cooley and Lohnes 1971). The criterion is that the first pair of factors has maximum correlation between the 2 sets of data. A second independent (orthogonal) pair of factors is constructed next and so on until all the common variation in the data sets is explained. The maximum number of pairs of factors is equal to the number of variables in the smaller set. In practice, however, pairs of factors are extracted until the canonical correlation between them is no longer significant. The analysis was conducted using the subprogram CANCORR of the SPSS package (Nie et al. 1970).

Nests were mapped in the 2 Swash Bay colonies by determining their angle and distance from a fixed point with a Keuffel and Esser alidade. In the Middle Marsh colonies mapping was done by triangulation with a Keuffel and Esser transit. Repeated measurements and comparisons with m tape readings showed that both techniques were accurate within 1 dm of the true nest location. Two-way radios (Johnson, Messenger 109) were also used by the person at the nest and the alidade or transit operator. Angle and distance of nest location were converted to X and Y coordinates with a pocket calculator and plotted on a map in the field. In this manner, a continuous check of nest positions was possible.

Height and density of vegetation and size of the colony prevented accurate mapping on Spectacle and Clark's islands. However, cooperators measured nearest neighbor nest distances with a meter tape in portions of each colony.

Dispersion patterns were assessed by the nearest neighbor analysis of Clark and Evans (1954). Spectacle and Clark's islands were excluded because data were incomplete.

The dominant plants were recorded for each colony. For the Virginia and North Carolina colonies, the dominant plant forms were mapped as outlines of individual bushes and/or trees, or as groups of plants with continuous canopy on a 5-m grid. The vegetation height was estimated by a 3-m stick, with marked dm intervals, held vertically. In bushes of uneven height an average height was calculated. A continuous check of the position of plants on the maps was made possible by reference to nests previously placed on the map. (Maps are available on request.)

The height and density of vegetation and the size of the colony again prevented the use of similar methods on Spectacle and Clark's islands. Simple line transects were used to estimate plant cover on Spectacle Island. Plant cover was not estimated at all for Clark's Island because of the abundance of poison ivy.

The study was undertaken during late July and August 1975, after the nests had already been located, identified and marked by cooperators monitoring reproductive success in early summer. Except for a few nests in Swash Bay, none were active at the time of our fieldwork, so at the time of measuring nest variables, we rarely knew the species that had occupied the nest, thereby reducing a possible bias. Our field crew varied from 3–8 persons.

In the Virginia and North Carolina colonies all marked nests were measured (Table 1). On Spectacle Island all Snowy Egret (*Egretta thula*) nests and a random sample of about one-third of all Black-crowned Night Heron (*Nycticorax nycticorax*) nests were measured (Table 1). On Clark's Island all nests (mainly Snowy Egrets and Glossy Ibises [*Plegadis falcinellus*]), within a ¼-ha plot were measured. In addition, 30 randomly sampled nests of the more dispersed Black-crowned Night Heron were measured. The number of nests measured was often greater than maximum-number-estimated-to-be-active-at-peak-nesting (see Osborn and

TABLE 3

CORRELATION OF VARIABLES ON THE FIRST 4 PRINCIPAL FACTORS AFTER VARIMAX ROTATION OF THE FACTOR MATRIX

	Factors[a]			
Variable[b]	I	II	III	IV
CRD	0.33	0.23	−0.12	−0.10
TOP	0.37	−0.16	0.11	−0.07
CTR	0.60	0.55	−0.04	−0.04
OUT	0.32	0.02	−0.21	−0.07
DEF	0.19	0.80	0.14	0.04
OPEN	−0.17	0.76	−0.12	−0.10
TIM	−0.15	−0.06	0.01	0.98
SUC	−0.13	0.01	0.97	0.01
Percent of total variance	37.1	18.1	12.4	11.4
Cumulative percent of total variance	37.1	55.2	67.6	79.0

[a] Factors are interpreted to be vegetation size (I), nest stability (II), nesting success (III) and time of nest initiation (IV).
[b] Abbreviations of variable neames are defined in Table 2.

Custer 1978) shown in Table 1, because nests from the entire nesting season were measured.

Data analysis was accomplished on a CDC 6500 computer at Michigan State University and with facilities at Patuxent Wildlife Research Center.

RESULTS

Factor analysis.—The factor analysis basically defined 3 aspects of wading bird nesting: vegetative characteristics, time of nest initiation, and nesting success. Of the 8 axes (factors) derived, 4 account for 79% of the variation. The loadings of the 8 variables on these 4 factors are shown in Table 3. The remaining 4 axes, accounting for only 21% of the variation, were omitted because of eigenvalues less than 1 (Cooley and Lohnes 1971). They were also not included in the final VARIMAX rotation.

The first axis is best termed a "vegetation size" factor since highest correlations are with GRD, TOP, CTR and OUT. The second axis reflects nest stability because of high correlations of CTR, DEF and OPEN. The highest correlations on the third axis are with SUC; TIM is the most highly correlated on the fourth. All other variables have very low correlations with these last 2 axes, designated the nest success factors and time of nest initiation, respectively.

Mean factor scores by species and colony are plotted for each factor in

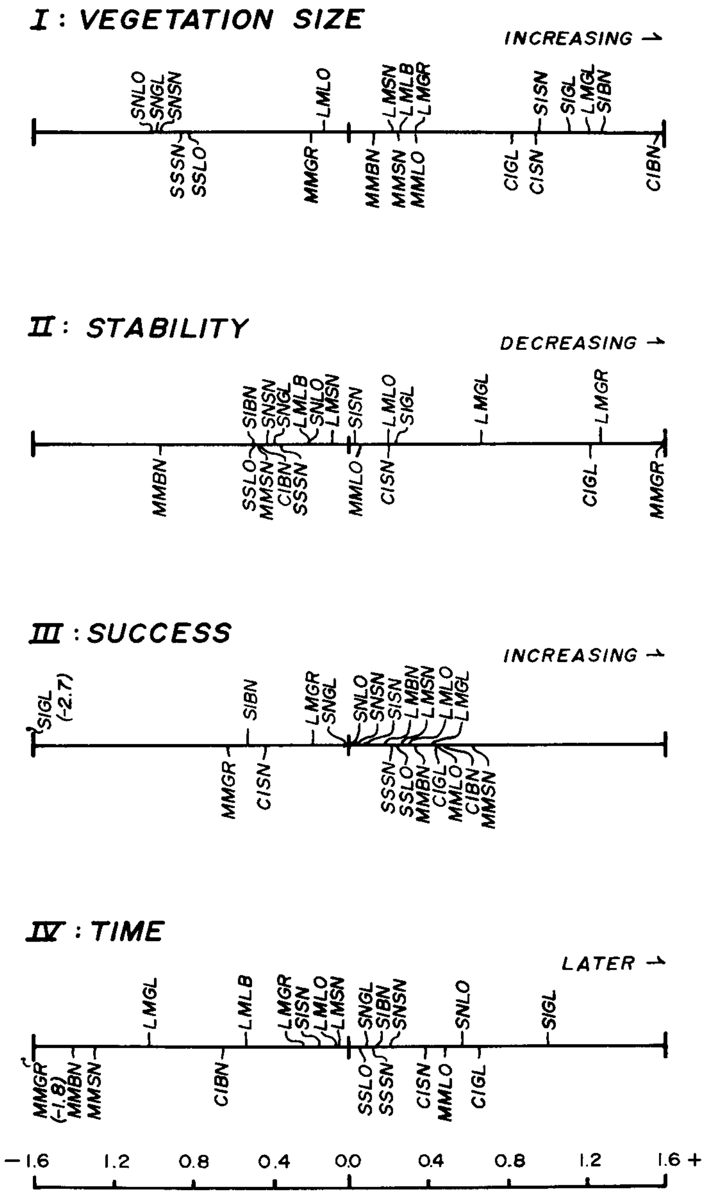

FIG. 1. Ordination of mean factor scores for each species in each colony for the 4 main factors. Abbreviations are for colony and species. The first 2 letters abbreviate the colony, the second 2 the species. Colonies are SN—Swash Bay NNE, SS—Swash Bay SSW, MM—Middle Marsh, LM—Lower Middle Marsh, CI—Clark's Island, SI—Spectacle Island. Species are: SN—Snowy Egret, LO—Louisiana Heron, LB—Little Blue Heron, BN—Black-crowned Night Heron, GR—Great Egret, GL—Glossy Ibis.

Fig. 1. By examining how means are grouped it is possible to determine if the factor is important as a possible characteristic of the wading bird species or whether it is the result of a colony's physical characteristics.

The vegetation size factor (Fig. 1) shows that species-colony means tend to be grouped by colonies. Thus the greatest amount of the variation accounted for by the statistical model appears to reflect directly the variation in plant size in nesting colonies, i.e., a colony's physical characteristics.

Species groups, rather than colonies as in the first factor, tend to sort out along the stability factor (Fig. 1 [II]). The most stable nests are of the Black-crowned Night Heron regardless of colony. The least stable nests are of the Great Egret (*Casmerodius albus*) in both colonies and the Glossy Ibis on Clark's Island and Lower Middle Marsh. The remaining species show a trend toward decreasing nest stability with colonies containing larger vegetation. An exception is the Snowy Egret with a slightly more stable nest at Middle Marsh than at either Swash Bay colony.

Patterns along the nesting success factor (Fig. 1 [III]) are less clearcut than for the previous factors. In general, Snowy Egrets, Louisiana Herons (*Hydranassa tricolor*), Little Blue Herons (*Florida caerulea*) and Glossy Ibises all have similar nesting success in colonies where they nest together. Two exceptions occur in the north where Glossy Ibises are noticeably more successful than Snowy Egrets—on Clark's Island and on Spectacle Island where the reverse is true.

For the last factor, time of nest initiation, no apparent pattern can be seen (Fig. 1 [IV]). Even the expected relationship of time of nest initiation to the latitude of a colony is not consistent.

Two-dimensional plots may also be examined for combinations of these factors since the statistical model derives them orthogonally. Because of the large amount of variability explained by the first 2 factors (55.2%), only vegetation size will be examined with nest stability (Fig. 2).

In the Swash Bay colonies Snowy Egrets, Louisiana Herons and Glossy Ibises nest in vegetation of very similar size and the nests are equally stable. Birds in the Middle Marsh colonies show large differences in stability of nest-sites they choose. Here, the Black-crowned Night Heron has very stable nests and the Great Egret very unstable nests (Fig. 2). Black-crowned Night Heron nests are more stable than the nests of all other species, but in Massachusetts their nest stability has decreased to a level comparable to that observed in the Swash Bay colonies for Snowy Egrets and Louisiana Herons. Great Egret nests are considerably less stable than other species even though other species in the Middle Marsh colonies nest in similar sized vegetation. In the Swash Bay colonies Snowy Egrets and Louisiana Herons have nests in similar sized vegetation and vary only slightly in stability. Little Blue Heron nests are found only in the Lower

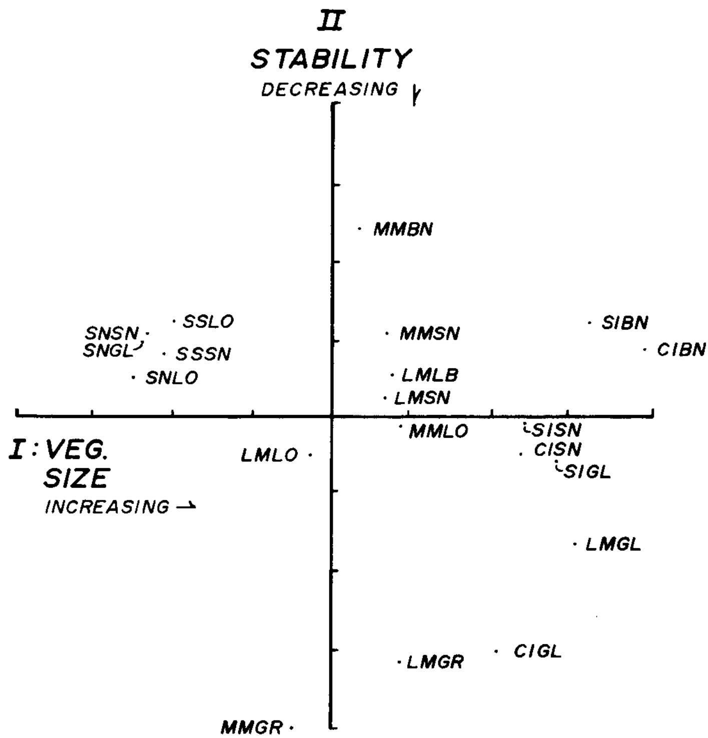

FIG. 2. Plot of mean factor scores for each species and colony of Factor I against Factor II. Abbreviations as in Fig. 1.

Middle Marsh colony where they are similar to Snowy Egret nests in both their stability and the size of vegetation in which they are placed.

The Glossy Ibis shows a marked decrease in nest stability in Lower Middle Marsh compared to Swash Bay (Fig. 2). Nests of this species are placed in the largest vegetation present on Lower Middle Marsh, which is similar in size with those in the Massachusetts colonies. However, Glossy Ibis are also often found nesting on the ground, even when there is vegetation present (Burger and Miller 1977). Their versatility in this respect may indicate that factors other than nest stability are important in choice of a nesting site.

Snowy Egrets on Clark's and Spectacle islands have lower stability in their nest-sites than in Swash Bay and Middle Marsh colonies. The overall pattern of each species is a consistent, but decreasing, stability of nest-

TABLE 4
THE STRUCTURE OF THE FIRST CANONICAL VARIATE

Variable sets[a]	Correlation with first canonical variate
Vegetation characters (independent)	
GRD	−0.89
TOP	−0.42
CTR	−0.61
OUT	−0.82
DEF	−0.12
OPEN	−0.12
Time and success (dependent)	
TIM	0.63
SUC	0.81

[a] Variable explanations Table 2.

sites with increasing vegetation size from the Swash Bay to Middle Marsh to Massachusetts colonies.

Vegetation characters and time and success of nests.—Factor analysis demonstrated that TIM and SUC are highly correlated with factors III and IV, respectively (Table 3), and therefore vary independently of each other. However, possible relationships between these variables and characteristics of the vegetation were suggested for at least the Great Egret. This was examined using canonical correlation. Table 4 shows the loading of variables on the only significant pair of canonical variates (canonical r = 0.35, $\chi^2 = 47.6$, df = 12). The canonical variate from the first (independent) variable set describes, as with the first factor in the factor analysis, the size of vegetation in which the nest is placed. GRD, TOP, CTR and OUT have large, negative correlation values. Both variables of the second (dependent) set are positively correlated with the other canonical variates suggesting that part of both time of nest initiation and nest success are related to the size of vegetation supporting the nest.

At least a part of the correlation is due to the poor nesting success shown by the Great Egret (Fig. 2) which tended to choose nest-sites that are exposed and unstable relative to the nests of other species. Also, the Great Egret nested very early in Middle Marsh. It should be noted that in the canonical model only 12% of the variation in nest placement is explained by timing and success of nest. We therefore feel that while the result is interesting, it is not general. We would not expect to see the same

TABLE 5

DISPERSION PATTERNS OF NESTS IN WADING BIRD COLONIES

	Parameters[a]						
Colony	N	A	ρ	$\bar{r}_A$	$\sigma_{\bar{r}_E}$	c	*P*
Swash Bay, SSW	96	256	0.375	0.431	0.043	−8.95	<0.001
Swash Bay, NNE[b]	211	2473	0.085	0.966	0.062	−12.11	<0.001
		(406)	(0.520)		(0.025)	(10.92)	(<0.001)
Middle Marsh	120	3675	0.033	1.629	0.132	−8.63	<0.001
Lower Middle Marsh	193	1400	0.138	1.106	0.051	−4.75	<0.001

[a] Parameters are: N = number of nests in colony; A = area of colony, in m^2; ρ = observed density of nest per m^2; $\bar{r}_A$ = mean nearest neighbor nest distance in meters; $\sigma_{\bar{r}_E}$ = the standard error of mean nearest neighbor nest distance when nests are randomly distributed; c = standard variate of the normal curve; *P* = probability of getting a deviation this great from random dispersion.

[b] Values in parentheses represent the exclusions of an unusable central portion of the colony in the calculations.

relationship in other wading bird colonies without specific qualifying conditions.

Summarizing, the factor analysis clearly distinguishes colonies based on the size of the vegetation used for nesting. Secondly, nest stability in the form of our measure of deflection, distance to the center and openness show consistent trends for a species regardless of the colony location. It is this factor that we feel characterizes how and where these wading birds choose their nesting sites. We will return to this important point in the discussion.

Dispersion of nest-sites.—Dispersion of nests within colonies was examined by nearest neighbor analysis (Clark and Evans 1954). All 4 colonies tested show significant aggregation of nests (Table 5), however, the test appears to be sensitive to what is defined as the area of a colony. In Swash Bay NNE, bushes with nests were nearly continuous around the perimeter of the colony. The center was occupied by grasses, forbs and a few dead bushes. If this central area is excluded the result shows a uniform dispersion of nests (Table 5, data in parentheses). All deviations from randomness are in the direction of clumping. An analysis of variance indicated that differences in the degree of departure from randomness were highly significant ($F = 336$, df = 3/616, $P < 0.001$).

The spacing of nests by species in relation to the nearest nest of any species shows a pattern that appears to be related to the average size of the vegetation in the colony (Table 6). In general, larger inter-nest distances occur in the colonies with larger vegetation.

The angle of exit from the nest was measured for all species in every colony to see if it was related to the spacing pattern or some other factor,

Table 6

Distance ($\bar{x} \pm$ SE[N]) (n) Between a Species Nest and the Nearest Nest or Any Wading Bird[a]

Colony	Species[a] GREG	SNEG	LOHE	LBHE	BNHE	GLIB
Swash Bay, SSW		0.44 ± 0.38 (51)	0.5 ± 0.06 (17)			
Swash Bay, NNE		1.0 ± 0.07 (99)	0.9 ± 0.10 (25)			0.9 ± 0.19 (8)
Middle Marsh	1.2 ± 0.10 (55)	0.5 ± 0.06 (11)	3.0 ± 0.80 (8)		3.4 ± 1.80 (9)	
Lower Middle Marsh	1.0 ± 0.07 (25)	1.0 ± 0.10 (32)	1.2 ± 0.10 (53)	0.9 ± 0.08 (12)	1.1 ± 0.51 (2)	1.1 ± 0.10 (9)
Clark's Island		1.6 ± 0.41 (10)			7.8 ± 3.40 (7)	0.9 ± 0.12 (10)
Spectacle Island		1.7 ± 0.52 (6)			1.6 ± 0.71 (5)	

[a] Species abbreviations are given in Table 1.

Table 7

Angle ($\bar{x} \pm$ SE[N]) (°) as Measured According to the Compass Bearing of the Exit From the Nest for Species of Wading Birds in 6 Atlantic Coast Colonies

Species[a]	Swash Bay SSW	Swash Bay NNE	Middle Marsh	Lower Middle Marsh	Clark's Island	Spectacle Island
GREG			299 ± 113 (25)	129 ± 103 (19)		
SNEG	207 ± 152 (35)	326 ± 126 (79)	235 ± 91 (3)	124 ± 109 (23)	92 ± 114 (26)	258 ± 88 (38)
LOHE	213 ± 76 (13)	54 ± 122 (17)	281 ± 60 (4)	143 ± 90 (26)		
LBHE				103 ± 112 (14)		
BNHE			315 ± 25 (2)		29 ± 106 (24)	75 ± 124 (39)
GLIB		105 ± 68 (4)		299 ± 62 (5)	323 ± 118 (15)	129 ± 81 (6)

[a] Species abbreviations Table 1.

TABLE 8

PERCENT COVER OF PLANT SPECIES SUPPORTING WADING BIRD NESTS AND THEIR USE BY WADING BIRDS IN 6 COLONIES ALONG THE ATLANTIC COAST

Colony	Plant species supporting nests	Relative cover in colony	Percent nests found in plant species						
			All nests[a]	GREG	SNEG	LOHE	LBHE	BNHE	GLIB
Swash Bay, SSW	highwater shrub (live)	77			94	90			100
	highwater shrub (dead)	<1			6	10			0
	other[b]	23			0	0			0
					(55)[c]	(20)			
Swash Bay, NNE	highwater shrub (live)	37			51	74			33
	highwater shrub (dead)	11			49	26			67
	other	52			0	0			0
					(103)	(23)			(8)
Middle Marsh	highwater shrub (live)	18	4	2	0			0	
	oak	8	43	56	34	88		43	
	yaupon	10	31	20	58	0		57	
	juniper	1	16	22	8	12		0	
	other	63	6	0	0	(8)		0	
			(115)	(55)	(12)			(7)	
Lower Middle Marsh	ground	8	2	3	0	0	0	0	0
	highwater shrub (live)	26	16	0	6	18	0	0	0
	palmetto (*Serenoa* spp.)	10	1	0	3	0	0	0	0
	pokeberry	10	1	0	6	0	0	0	0
	poison ivy	10	2	0	0	0	0	0	0
	bay (*Myrica* spp.)	1	0	12	0	0	6	0	0
	oak	27	44	31	50	40	83	100	44
	yaupon	10	25	31	25	29	11	0	23
	juniper	10	9	23	10	0	0	0	33
	other	20	0	0	0	0	0	0	0
			(308)	(26)	(32)	(53)	(18)	(2)	(9)
Clark's Island	Virginia creeper (*Parthenocissus* spp.)				0			0	4
	arrow wood				26			19	70
	shadbush				10			2	4
	highbush blueberry				30			7	9
	staghorn sumac				4			2	4
	cherry				4			10	9
	pine (*Pinus* spp.)				0			2	0
	juniper				26			58	0
					(23)			(43)	(23)
Spectacle Island	ground[d]				0			1	0
	raspberry (*Rubus* spp.)	3			23			2	0
	rose (*Rosa* spp.)	2			4			0	0
	staghorn	77			18			15	0

TABLE 8
CONTINUED

Colony	Plant species supporting nests	Relative cover in colony	All nests[a]	GREG	SNEG	LOHE	LBHE	BNHE	GLIB
Spectacle Island (continued)	buckthorn	3			15			34	71
	apple	1			2			10	0
	pear (*Pyrus communis*)[e]	0			0			1	0
	cherry	2			36			30	29
	poplar	4			0			5	0
	linden (*Tilia* spp.)	0			2			0	0
	tree-of-heaven (*Ailanthus* spp.)	5			0			2	0
	other	3			0			0	0
					(47)			(122)	(7)

[a] Included all species and nests not identified to species. Clark's and Spectacle islands have no figure for this category because only a sample of nests was made.
[b] Other includes grass, composites, etc., that were judged not suitable as nesting supports.
[c] In parentheses are the number of nests measured for the category.
[d] Not measured—little ground cover at all.
[e] Zero percent cover estimated by line transect; plants were present in the colony and some were used by birds.

such as shading from the sun. We predicted that nests would be opening to the north if shading was important. However, the nest exit angles of all species in every colony were random (Table 7, test of angular dispersion, Zar 1974:310). If the nest exit angle was a function of interactions with the nearest neighbor, one would expect them to be oriented in different directions. No significant relationship between exit angles emerged that would suggest that openings were selected to avoid leaving or entering in the path of the nearest nest.

In the Swash Bay colonies, the vegetation used for nesting was high-water shrub, comprising the major part of both of these colonies (Table 8). The birds nested exclusively in either dead or living shrubs, but preferred living ones. These colonies appeared to be "full," that is, very little additional nesting space appeared to be available. In the 2 Middle Marsh colonies, where there is a higher diversity of plants, the waders nested in the higher nesting sites offered by oak, yaupon and juniper, rather than in highwater and other shorter shrubs. This may have been in response to tidal or storm flooding, or predation by mammals such as rats (*Rattus* sp.) and raccoons (*Procyon lotor*). Middle Marsh appeared to have considerable unused nesting sites, whereas Lower Middle Marsh had fewer unused sites. A greater diversity of supporting plant species occurred in the Massachusetts colonies, although this was not accompanied by an increase in wading bird species. Our impression was that many potential nesting sites were unused in both colonies.

Using percent cover as an estimate of the availability of nest-sites of all species combined in the Middle Marsh colonies, a Chi-square test yielded significant deviations (all $P < 0.005$) from the expected pattern (i.e., random). The same result is obtained for each species in these colonies, although the smaller sample size makes the result less reliable. The same trend was found for Spectacle Island, with cherry, buckthorn and staghorn sumac being the most frequently used nesting supports. Staghorn sumac appears to be avoided, whereas the other 2 support species are selected above their proportion of the cover. Wading bird species occurring on Spectacle Island were not tested for their nest support preference because we took subsamples within the colonies.

DISCUSSION

Nest-site characteristics.—The general applicability of our results is difficult to assess because only a few studies are available for comparison. McCrimmon (1978) studied a colony of egrets and herons in 1974 on Phillip's Island, only a few km north of our Middle Marsh colonies. He used a principal component analysis to examine 12 nest-site characters for 5 species of wading birds (Great Egret, Snowy Egret, Little Blue Heron, Cattle Egret [*Bubulcus ibis*] and Louisiana Heron). Six of his variables closely resemble those used in this study; those relating to position of the nest in the vegetation and vegetation size (nest height, height of vegetation above the nest, distance from center, degree of openness above the nest, diameter of nest branch and diameter of the nest tree 1 m above the ground). He found that 4 components accounted for 69% of the variation in the model. Two of his components (factors I and IV) are basically similar to our vegetation size (factor I) and nest stability (factor II). McCrimmon did not use a measure of nest deflection as we did, but the variables of distance to the nest from the center, diameter of nest branch and the degree of openness above the nest were measured and are the basis for the similarity of his fourth and our second factor in the statistical model. McCrimmon's remaining 2 factors (II and III) involve "accessibility" and "protection" of the nest by the surrounding vegetation and they appear to be specific to the Phillip's Island colony. We do not have comparable data for these factors.

Comparing our factor I with McCrimmon's factor I (vegetation size) shows little similarity in the magnitude or order of individual species' factor scores along the axis in the Middle Marsh colonies. Either the variables measured are different enough in the 2 studies to produce this effect or the size of the vegetation used for nesting is not a consistent feature for

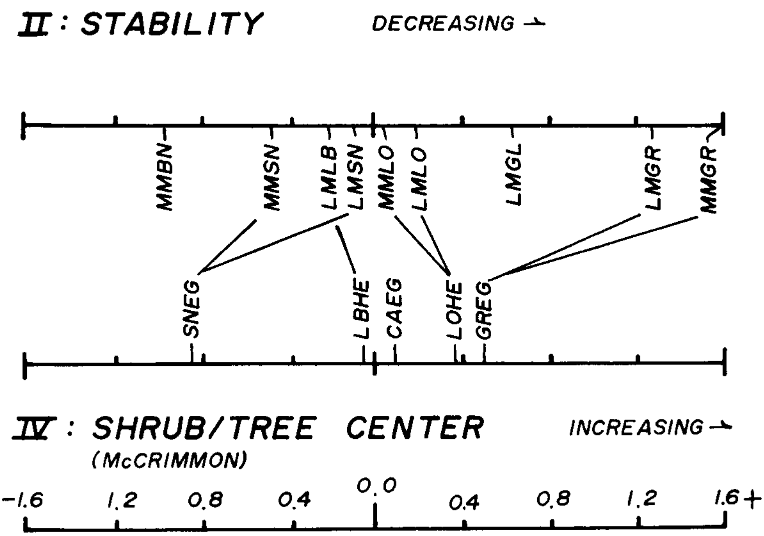

FIG. 3. A comparison of Factor II in our study for the species nesting in the 2 Middle Marsh colonies to McCrimmon's (1978) Factor IV. Lines connect the species. Abbreviations for the stability factor are the same as those in Fig. 1. Abbreviations in McCrimmon's Factor IV are the same as those of Table 1.

these species. We suspect the latter because of the large range of vegetation size available for nesting and the apparent lack of selectivity for vegetation size in other colonies by the species studied.

The order of species along the nest stability factor (factor II) in our study and factor IV in McCrimmon's study correspond. The only species out of place is the Little Blue Heron in Lower Middle Marsh (Fig. 3) but the factor score is not significantly different from the adjacent Snowy Egret. The differences in the magnitude of factor scores between the 2 studies on these factors are probably the result of different variables measured and measuring techniques. Nevertheless, the pattern is very striking and it is our interpretation that the basis for the similarity of the stability factor in our study and McCrimmon's is a species-specific preference for a stable nest-site. It is noteworthy that the courtship display of the male of all the species studied here is centered on the nest-site. Jenni (1969:249) noted that the male ". . . performs his displays on a sturdy site offering considerable support, and the nest was usually built in the same place." Most of the behavior of the mated pair also occurs on the display and nest-site (Jenni 1969, Burger 1978). It remains to be shown that the patterns in nest-site stability found in our study and McCrimmon's are consistent for other colony sites or for more than 1 year within colonies.

TABLE 9

MEAN NEST HEIGHT (M) FOR 6 SPECIES OF WADING BIRDS ($\bar{x}$ ± SD [N])

	Colony					
	Swash Bay		Middle Marsh			
Species	SSW	NNE	Middle	Lower Middle	Clark's Island	Spectacle Island
Snowy Egret	0.14 ± 0.05 (51)	0.12 ± 0.06 (103)	1.11 ± 0.38 (11)	1.1 ± 0.53 (30)	2.2 ± 0.49 (34)	2.2 ± 0.94 (47)
Louisiana Heron	0.14 ± 0.06 (18)	0.12 ± 0.05 (23)	1.0 ± 0.4 (8)	0.81 ± 0.28 (55)		
Little Blue Heron				1.5 ± 0.22 (17)		
Black-crowned Night Heron			1.3 ± 0.35 (8)		2.6 ± 0.93 (30)	2.6 ± 0.91 (43)
Great Egret			1.7 ± 0.46 (53)	1.7 ± 0.74 (28)		
Glossy Ibis		0.11 ± 0.05 (8)		1.2 ± 0.63 (9)	2.4 ± 0.34 (21)	2.9 ± 0.34 (6)
Mean vegetation height[a]	0.42 ± 0.08 (71)	0.36 ± 0.11 (134)	2.12 ± 0.63 (80)	2.07 ± 0.71 (140)	4.70 ± 1.49 (85)	4.74 ± 1.47 (95)

[a] Of plants with nests.

Summarizing, our analysis points to the stability of the nest-site as a key character for choice of a site. The courtship and mating behavior of herons and egrets within their territories may be the mechanism by which the stability of the nest-site is assessed and either accepted or rejected for a more (or less) stable site.

Social factors and nest-site selection.—Jenni (1969) noted that vertical stratification occurred in the heronry he studied, but the stratification was more or less pronounced or absent depending on the year. New sites were selected each year by most species because the previous year's nests had fallen apart during the nonbreeding season. Burger (1978) has suggested that vertical stratification occurs as a means of reducing competition for nest-sites, especially in vegetationally homogeneous colonies. However, in the Swash Bay colonies, where the vegetation was homogeneous, essentially no vertical stratification occurred, probably because of the low height (1 m). The most diverse colony sites (MM, LMM) in terms of both vegetation and bird species showed increased stratification in vertical nest position (Table 9). McCrimmon (1978) also found a similar pattern for the Phillip's Island Colony. If nest-sites are selected on the basis of their stability, vertical stratification may or may not be a result, depending on a species preference and vegetation in the colony. If the stability of sites is correlated with their vertical position, then stratification would be a consequence of selecting stable sites. However, if nest-site stability and vertical position are poorly correlated, which may occur in colonies like the ones Jenni (1969) studied, then vertical stratification is not likely to be consistent from colony to colony, or even for different years in the same colony.

One aspect with which we have not dealt is the effect that social interactions may have on nest-site selection. Burger (1978) has suggested that large species dominate the smaller ones and force smaller species to nest lower in the vegetation than they otherwise would. This, in effect, produces vertical stratification of species in a colony according to body size. Body size here refers to body length with the neck extended (a measure of interaction distance), not body weight (Burger 1978). However, our data do not show the predicted pattern in every colony. The Glossy Ibis nested higher than the longer-bodied Snowy Egret in the 2 Massachusetts colonies (Table 9). Snowy Egrets nested at the same height as the longer Louisiana Heron in the Middle Marsh colonies. The longest species, the Great Egret, nested the highest of all species in the Middle Marsh colonies, but they were only 70 cm higher on the average, which is well within the estimated interaction distance (2 m) for the Great Egret. These inequities could be explained by postulating that vegetation factors prevent the effects of social interactions from being fully realized. As our data on vegetation used as nest support suggest (Table 8), nearly all of the birds were nesting in the most rigid plants while other areas of the colony or other plant types were not used. This resulted in the consistent pattern of clumping of nests we found (Table 5), since the rigid plants tended also to be clumped. The Swash Bay colonies were "homogeneous" in the sense that *Iva* was the only shrub present, but the pattern of nesting was still clumped because only certain parts of the vegetation could support nests, namely the lower parts close to the center of the shrub. As pointed out earlier, the nests in the NNE colony were actually highly uniform in dispersion (if the unvegetated center of the colony is excluded from the area) (see Table 5), a pattern which matched the older and more uniformly spaced *Iva* compared to the SSW colony. These results suggest that the structure of the vegetation strongly influenced nest dispersion and probably also the position of the nest-site. Perhaps social interactions modify the pattern only when: (1) a colony is fully occupied, i.e., has no more vegetation for nesting and (2) vegetation allows a wide range of nest placement, i.e., acceptable sites occur at all levels within the vegetation. The Swash Bay colonies met the first condition, in that every bush was used and that inter-nest distances were 0.4–1.0 m, but not the second, since no vertical stratification occurred. Lower Middle Marsh colony met both conditions and vertical stratification was pronounced. Horizontal separation was also greater than the Swash Bay colonies ($\bar{x}$ = 1.6 m). Although extensive areas within the Middle Marsh colony were not used for nesting, nest-sites were stratified. Again this seems to be due to the vegetation since the 3 main species of waders did not use the same species of plant for nesting and, therefore, tended to be horizontally segregated. Thus, the vertical stratification was still manifested even though the vegetation height was not different for the plant species used and the horizontal segregation precluded social interactions involving nest height.

Neither of the Massachusetts colonies was fully occupied and vertical stratification was minimal (Table 9). The various species tended to nest in spatially distinct parts of the colony in different species of plants (Table 8). Inter-nest distance tended to be high (Table 6). The vegetation in these colonies was the highest and most varied in height of all colonies studied.

Thus, the dispersion pattern of nests is probably more strongly influenced by the availability of suitable vegetation in the colony than by social interactions. Birds appear to nest in any available vegetation that will support a nest. Where only a limited diversity of nest support species are present, nests are placed according to stability requirements. This may result in stratification if a large enough vertical range of suitable sites exist and/or social interactions are intense. Nests may not be vertically or horizontally stratified despite social interaction, even in fully occupied colonies, if the vegetation does not permit it.

However, that does not mean that social factors play no role in the colonial nesting habit of wading birds. Social attraction brings individuals together to nest and brings a variety of species together in multi-species colonies. Krebs (1974) has argued that the colony may serve as an information center to increase feeding rates of individuals and Custer and Osborn (1978) present indirect evidence that supports this hypothesis. Within the colonies we studied social factors had little consistent (measurable) effect on where nests were placed. The vegetation and the preferences of species for particular nest-site characteristics, most notably their stability, was seemingly critical to the selection of nest-sites.

SUMMARY

Nests of 5 species of wading birds were identified and marked during the breeding season at 6 locations from Massachusetts to North Carolina. At the end of the breeding season 12 characteristics of nest-site location were measured. Nest locations were mapped to examine dispersion and nearest neighbor relationships. Multivariate analyses were used to describe and compare sites and species.

We found that variations in nest-sites between colonies were greater than between species; colonies differed mainly in the variety and size of vegetation; birds preferred to nest in vegetation that offered relatively stable nest-sites; and the dispersion of nests in the colonies was related to vegetative patterns. The interaction of these factors with the number of bird species and the abundance of birds in the colony seemed to determine whether nest-sites were stratified, segregated or randomly distributed.

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