NEST SITE CHARACTERISTICS AMONG FIVE SPECIES OF HERONS ON THE NORTH CAROLINA COAST

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ABSTRACT.—A study of nest site characteristics of five species of herons and egrets on a North Carolina coastal heronry using principal component analysis revealed four components describing sampled nest sites: vegetation structure, accessibility, protection, and shrub/tree-center distance. Comparison of nest sites on the basis of component scores revealed that nest sites of Great Egrets were significantly different from those of the other species. Comparison of mean vectors revealed nest site differences among most of the smaller species. The study suggests that the smaller species may be reducing competition for nest sites through differential use of environmental variables associated with the site. Confirmation of the biological significance of these differences will require additional studies.

Great Egrets began nesting the earliest, starting in late March. Cattle Egrets began nesting somewhat later than most other species and were more temporally dispersed in nesting, continuing into June. Horizontal partitioning of nest sites occurred, Great Egrets, Snowy Egrets and Cattle Egrets nesting in significantly different proportions in different areas of the heronry.

Great Egrets nested significantly closer to other Great Egrets than to individuals of other species. The smaller herons generally nested closer to contraspecifics than to conspecifics. There was no tendency for the smaller species to nest in exclusively conspecific groups. Conspecific nesting in Great Egrets is most likely related to the unique nest site of the species. *Received 16 July 1976, accepted 17 January 1977.*

WHERE herons and egrets are abundant, species commonly nest in colonies containing hundreds to thousands of pairs in relatively limited areas and in high density. The nest sites of many species appear similar and species may compete interspecifically for the available resources. Differential division of the nest site resources may reduce competition among species. Several studies have suggested this (Meanley 1955, Ralph and Ralph 1958, Lowe-McConnell 1967, Dusi 1968), but most rely on qualitative assessments of nest site differences. Jenni (1969) reported more quantitative information on vertical stratification and some horizontal zonation, as well as partitioning of food resources, among several species nesting in a central Florida heronry. Burger (in press) has noted vertical nest site stratification in colonies characterized by vegetation of uniform appearance. In one such colony in New Jersey, she suggests that nest height and inter-nest distances may be predicted from aggressive interactions among species.

This study attempted to measure various nest site characteristics to determine the extent of resource division among Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Cattle Egrets (*Bubulcus ibis*), Little Blue Herons (*Florida caerulea*), and Louisiana Herons (*Hydranassa tricolor*) nesting in a colony on the mid-coast of North Carolina during 1974. I described each nest site by physical variables judged potentially important to birds selecting nesting sites. I applied several multivariate statistical techniques to characterize the major independent groups of habitat variables associated with nest sites and to assess the separation of species' nest site

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TABLE 1. Density (mean number of plants/m^2 in vegetation sampling subquadrats) and frequency (percent of 12 subquadrats in which a plant species was found) of the species of shrubs and trees found in study areas on Phillips Island and the Annex. *Iva*, *Ilex*, *Myrica*, and *Baccharis* were shrubby species. *Juniperus* assumed both shrub and tree-like configurations. *Morus*, *Broussonetia*, and *Pinus* were trees

Species	Density	Frequency
PHILLIPS ISLAND		
Marsh elder (*Iva frutescens*)	.005	8
Yaupon (*Ilex vomitoria*)	.250	92
Eastern red cedar (*Juniperus virginiana*)	.026	50
White mulberry (*Morus alba*)	.016	42
Paper mulberry (*Broussonetia papyrifera*)	.049	50
ANNEX		
Groundsel bush (*Baccharis halimifolia*)	.012	25
Yaupon (*Ilex vomitoria*)	.002	8
Wax myrtle (*Myrica cerifera*)	.250	100
Eastern red cedar (*Juniperus virginiana*)	.019	42
Loblolly pine (*Pinus taeda*)	.002	8

microhabitats. I also measured distances between nests, time of nest building, and differential dispersion among species within certain areas of the heronry.

METHODS

The study area was a two-island heronry complex approximately 1.5 km N of Morehead City, North Carolina. Phillips Island was formed primarily from the deposition of dredge material in the early 1900's. Nest sites on the Phillips Island heronry were in a maritime shrub thicket of approximately 1.5 ha. The density and frequency of shrubs and trees in three quadrats on Phillips Island are presented in Table 1. Each study area was sampled by a randomly positioned 24-m transect along which four 6 × 6-m vegetation sampling subquadrats were alternated. Only plants above 1 m in height were sampled.

The Annex, approximately 500 m N of Phillips Island, was formed by dredging in the 1950's. Herons have nested on the island since the 1960's. The vegetation of the heronry on the Annex is a crescent-shaped maritime shrub thicket of approximately 4 ha. Table 1 lists the importance of various plant species on the Annex.

The Annex and Phillips Island are considered a single heronry complex and data for nest site characteristics for nests on each island have been combined for analysis. There are several justifications for this: (1) the islands are located in very close proximity and in 1974 and previous years both were used by all species reported in this study; (2) as vegetation on the Annex became more favorable for nesting, vanguards from the previous nesting populations occupying Phillips Island probably emigrated to the Annex; (3) during the 1974 nesting season, considerable movement of birds occurred between the two islands at times when display areas and nest sites were being selected and when new groups of apparently reproductively receptive birds were arriving; (4) early in the nesting season roosting birds often landed at both islands prior to choosing a final roosting site; and (5) combining data increases the range of potential variation in nest sites available for selection by birds and for analysis in this study.

On both the Annex and Phillips Island I established three 18× 24-m quadrats. The size and location of the quadrats were restricted by the field of vision from an observation tower. On the Annex, the quadrats were at randomly selected points on the interior perimeter of the vegetation, an area of intense nesting activity during 1974. The locations of the Phillips Island quadrats were selected on the basis of the configuration of the vegetation, knowledge of areas where birds had bred in the past, and the need to make behavioral observations within the nesting quadrats. I sampled 50–75% of the vegetation on Phillips Island in which nests were built during 1974. Unsampled areas in which the birds built nests appeared vegetationally very similar to the sampled areas. On both islands, nests built or reoccupied within each quadrat were numbered, identified (when possible) by species, and located (to the nearest 0.1 m) within the quadrat by a set of three Cartesian coordinates: location on the 18-m side, location on the 24-m side, and height above the ground.

I visited each quadrat once each week and marked all newly-built or occupied nests with numbered plastic tape. Adults would quickly leave the nest upon my approach, making identification of nests on the basis of adults impossible for most nests. After the young hatched, I identified nests according to species on

TABLE 2. Means, standard deviations, and coefficients of variation (CV) of nest site variables for 41 Great Egrets, 63 Snowy Egrets, 76 Cattle Egrets, 33 Little Blue Herons, and 39 Louisiana Herons nesting on the Phillips Island–Annex heronry in 1974. The overall means were calculated from the 252 nest sites of all species. Methods of measurement are described in the Appendix

Variable		Great Egret	Snowy Egret	Cattle Egret	Little Blue	Louisiana Heron	Overall species
Nest height above ground (m)	$\bar{x}$	4.38	2.27	2.26	2.25	2.03	2.57
	SD	.90	.54	.38	.63	.40	.98
	CV	21	24	17	28	20	38
Height of vegetation at nest (m)	$\bar{x}$	5.73	3.92	3.83	3.86	3.67	4.14
	SD	1.35	.59	.63	.59	.66	1.05
	CV	24	15	17	15	18	25
Vegetation openness above nest (%)	$\bar{x}$	88.88	42.00	53.44	43.56	35.27	52.24
	SD	15.74	28.32	30.86	26.10	27.53	32.01
	CV	18	67	58	60	78	61
Mean vegetation openness around nest (%)	$\bar{x}$	54.62	11.69	10.08	9.99	9.64	17.65
	SD	11.25	10.47	8.55	9.73	11.18	19.16
	CV	21	90	85	97	116	109
Transformed mean vegetation openness around nest	$\bar{x}$	7.35	3.10	2.89	2.84	2.69	3.63
	SD	.80	1.46	1.32	1.40	1.57	2.12
	CV	11	47	46	49	59	58
Mean vegetation density 1 m around nest	$\bar{x}$	.73	2.43	2.24	2.11	2.03	1.99
	SD	.62	1.65	1.53	1.40	1.51	1.54
	CV	86	68	68	66	75	77
Transformed mean vegetation density	$\bar{x}$	.73	1.47	1.40	1.39	1.34	1.30
	SD	.44	.54	.53	.44	.50	.56
	CV	60	37	38	32	37	43
Vegetation density 1 m above nest	$\bar{x}$	.80	3.46	2.91	3.76	2.97	2.83
	SD	1.52	3.08	2.58	2.54	2.01	2.65
	CV	189	89	89	68	67	94
Transformed vegetation density above nest	$\bar{x}$	.54	1.57	1.41	1.77	1.57	1.38
	SD	.73	1.00	.96	.80	.71	.96
	CV	135	63	68	45	45	69
Diameter of nest branch (cm)	$\bar{x}$	5.93	4.18	3.73	3.48	3.49	4.13
	SD	2.14	1.58	1.43	1.23	1.46	1.78
	CV	36	38	38	35	42	43
Diameter of nest tree (cm)	$\bar{x}$	23.94	6.77	5.84	5.67	6.17	9.05
	SD	11.73	2.86	2.36	1.74	4.84	8.54
	CV	49	43	40	31	78	94
Transformed tree diameter	$\bar{x}$	4.73	2.55	2.38	2.35	2.40	2.80
	SD	1.28	.51	.43	.42	.67	1.09
	CV	27	20	18	18	28	39
Distance of nest to tree center (m)	$\bar{x}$	1.57	.72	1.18	1.17	1.29	1.14
	SD	1.02	.50	.73	.71	.81	.79
	CV	65	70	62	61	63	69
Number of supporting branches	$\bar{x}$	4.22	3.79	3.63	3.00	3.44	3.65
	SD	1.17	1.27	1.03	1.22	1.48	1.26
	CV	28	34	28	41	43	34
Distance to nearest open space (m)	$\bar{x}$	3.83	6.25	6.54	6.62	6.88	6.09
	SD	2.10	3.20	2.92	3.54	3.07	3.14
	CV	55	51	45	54	45	52
Distance to heronry edge (m)	$\bar{x}$	10.56	13.50	15.93	13.61	15.82	14.13
	SD	2.75	4.64	5.28	4.46	5.68	5.09
	CV	26	34	33	33	36	36

the basis of morphological characteristics of the young (Dusi 1966, McVaugh 1972, Mitchell Byrd pers. comm.).

I marked 380 nests: 83 on Phillips Island, 297 on the Annex. Of these, 265 (70%) of the marked nests were eventually identified to species. Ten of these were Glossy Ibis (*Plegadis falcinellus*) and three were

TABLE 3. Rotated component matrix for 12 nest site variables. The matrix has been achieved through rotation by a varimax criterion. Each component is an independent dimension characterizing the nest sites birds nesting in the Phillips Island–Annex heronry complex

	Component			
Variable	Vegetation structure	Accessibility	Protection	Shrub/tree-center distance
Nest height above ground	.86[a]	.17	.24	.15
Height of vegetation at nest	.84[a]	−.07	.26	.14
Vegetation openness above nest	.28	.44	.57[a]	.04
Transformed mean vegetation openness	.60[a]	.52[a]	.40	.01
Transformed mean vegetation density	−.27	.11	−.66[a]	.11
Transformed above nest vegetation density	−.11	.00	−.77[a]	−.04
Diameter of nest branch	.52[a]	.10	.40	−.33
Transformed tree diameter	.82[a]	.20	.29	.18
Distance of nest to tree center	.15	.05	−.06	.91[a]
Number of supporting branches	.18	.67[a]	−.37	−.01
Distance to nearest open space	.03	−.81[a]	−.12	−.03
Distance to heronry edge	−.65[a]	−.03	.29	.37
Percent variance	41	20	25	14

[a] Indicates the component accounts for greater than 25% of variance of variable.

White Ibis (*Eudocimus albus*) nests, too few to permit meaningful analysis; these were dropped from subsequent analysis. Measurements of nest site characteristics were taken on 252 nests of five species (Table 2). Identified nest sites on the Annex were measured in August and September. Nest sites on Phillips Island were measured in November when leaves had fallen from the deciduous trees and the appearance of the vegetation was like that in early spring, at the time of site selection. Measurement methods are described in the Appendix.

To reduce the number of dimensions for description and comparison of nest sites of the five species, a principal component analysis was performed using data for each nest site of all of the species. Table 2 presents the means, standard deviations and coefficients of variation for distributions of variables used to consider nest sites in the multivariate analyses that follow. The overall species distributions, which had the greatest coefficients of variation, were also positively skewed. Outliers of the distribution could affect the mean and other statistics, leading to poorer results in the principal component analysis, which depends on the distribution of variables over all species for its solution. Square-root transformations of mean vegetation openness around the nest, mean horizontal vegetation density, above-nest vegetation density, and tree diameter produced the most satisfactory results in the principal component analysis. Each of the eight non-transformed and four transformed variables was significantly correlated with at least one other variable (H_0:r = 0.00).

The principal component solution rotated by a varimax criterion is presented in Table 3. A relatively rigorous criterion was set whereby variables having at least 25% of their variation accounted for by a component (component loading of 0.50 or greater) would be used to identify that particular component. The total solution accounts for 69% of the variation in data: of that, Component 1 accounts for 41%, Component 2 accounts for 20%, Component 3 accounts for 25%, and Component 4 accounts for 14%.

A chi-square test (Kendall and Stuart 1961) showed significant heterogeneity of within-group covariance matrices (P < .001). Although discriminant functions could be calculated, associations of variables on the functions were not strong, making interpretation of the functions and comparisons among species difficult. Paired comparison of the mean vectors of species is possible, however. For each species, the mean vector was composed of the means for that species of all variables used for the principal component analysis. A chi-square statistic (see Anderson 1958) compared the differences of mean vectors among species where the variance of mean differences is based on the large sample approximation. The test does not assume homogeneous within-group covariance matrices.

The three-dimensional metric coordinates for each nest permitted calculation of Euclidian inter-nest distances. Distances to the nearest nest of the same species built during the same or previous weeks were examined. However, calculations of distances between nests of each species and each other species might reflect not only differences in nest site requirements or interspecific interactive processes such as aggression and competition, but also would be related to differences in the total population sizes of the various species nesting in the heronry. To facilitate comparison of interspecific with intraspecific inter-nest distances, the

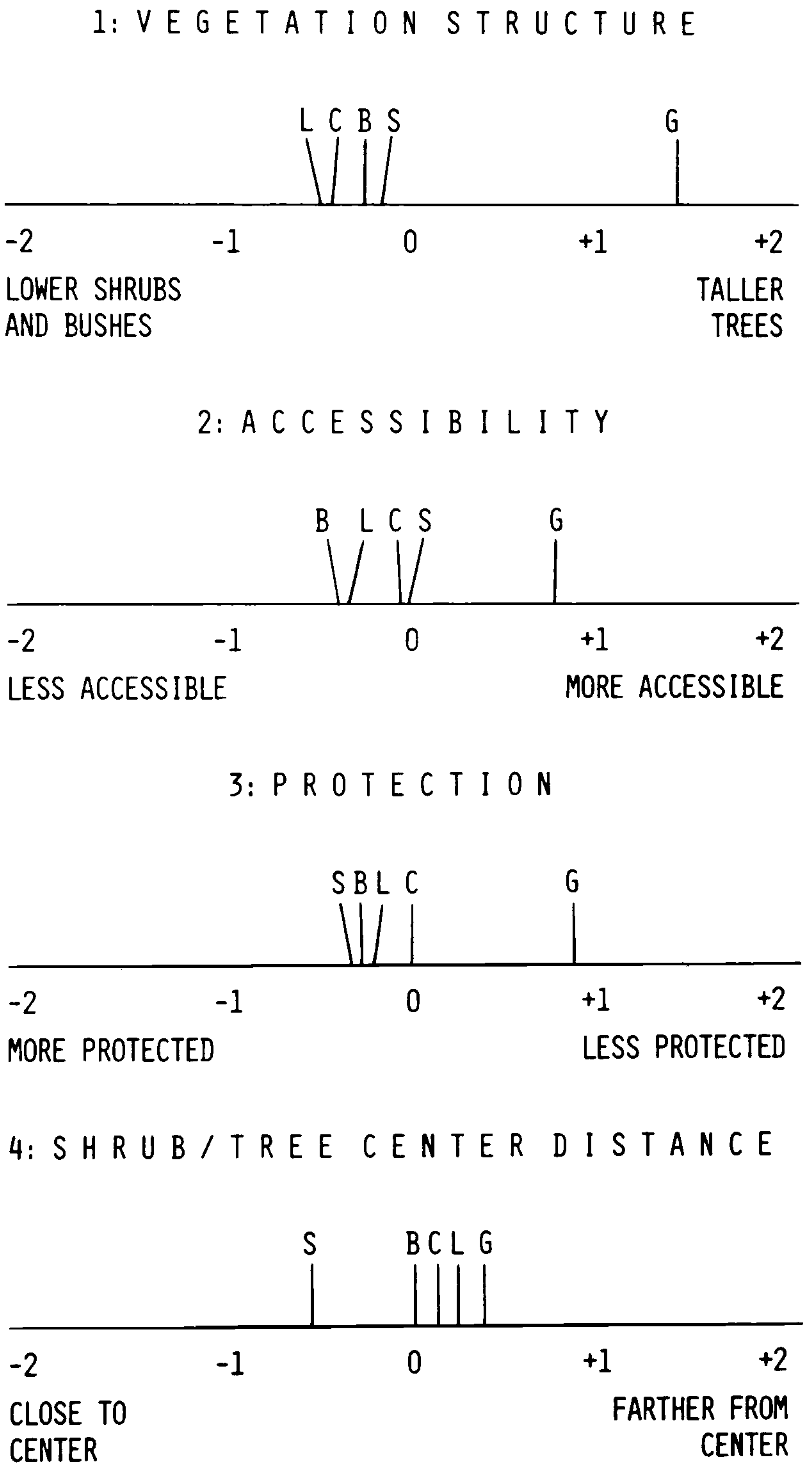

Fig. 1. Ordination of mean component scores for each species on four principal components. G = Great Egret, S = Snowy Egret, C = Cattle Egret, B = Little Blue Heron, L = Louisiana Heron.

TABLE 4. Mean component scores and results of comparisons among species on each component. Means for each species are ordinated on each component in Fig. 1

	Vegetation structure		Accessibility		Protection		Shrub/tree-center distance	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Great (G)	1.60	.90	.74	.66	.87	.66	.36	1.26
Snowy (S)	−.14	.66	−.02	1.12	−.32	1.03	−.54	.73
Cattle (C)	−.42	.65	−.05	.90	0.00	.92	.13	.97
Little Blue(B)	−.23	.68	−.39	.83	−.27	.92	.01	.91
Louisiana (L)	−.45	.64	−.32	1.03	−.18	.97	.22	.88

INTERSPECIES COMPARISONS[a] (Satterthwaite's Correction)

Vegetation structure

	G	S	C	B	L
G	X	<.001	<.001	<.001	<.001
S		X	<.025	ns	<.025
C			X	ns	ns
B				X	ns
L					X

Accessibility

	G	S	C	B	L
G	X	<.001	<.001	<.001	<.001
S		X	ns	ns	ns
C			X	ns	ns
B				X	ns
L					X

Protection

	G	S	C	B	L
G	X	<.001	<.001	<.001	<.001
S		X	ns	ns	ns
C			X	ns	ns
B				X	ns
L					X

Shrub/tree-center distance

	G	S	C	B	L
G	X	<.001	ns	ns	ns
S		X	<.001	<.005	<.001
C			X	ns	ns
B				X	ns
L					X

[a] Minimum level for rejection of $H_0 = P < .01$.

Euclidian distance of each nest to the nearest nest of any other species built within the same or previous weeks was evaluated. This general interspecific inter-nest distance avoids the difficulties associated with density differences among species.

RESULTS

PRINCIPAL COMPONENT ANALYSIS

The principal component solution describes patterns of the environmental characteristics of the sample of nests from this heronry on the basis of four independent dimensions rather than 12. Components may be defined by a concise description of the common features associated with the variables loading upon them. Component scores for each nest site were calculated (Rummel 1970) and species' mean component scores are ordinated in Fig. 1. Table 4 presents the results of multiple comparisons among species on each component. Bartlett's test indicated significant heterogeneity of variance among species on two components (Component 2 $\chi^2 = 14.23, P < .01$; Component 4 $\chi^2 = 15.54, P < .005$). Satterthwaite's (1946) correction for t-tests was applied to comparisons of mean component scores and basic variable values among species. The statistic was appropriate whether variances were homogeneous or not (see Snedecor and Cochran 1967). Because of multiple comparisons among species, the significance level was set at $P < .01$.

Component 1: Vegetation structure.—Variables loading on Component 1 were: Nest Height above Ground, Height of Vegetation at Nest, Transformed Mean Vegetation Openness around Nest, Diameter of Nest Branch, Transformed Diameter of Nest Tree, and the inverse of the Distance to Heronry Edge. Component 1 deals with the general size, structure, and appearance of the vegetation in which the nests were

TABLE 5. Comparisons of mean vector differences among five species of herons and egrets. The mean vectors are composed of the 12 variables used in the principal component analysis. For comparison, d.f. = 12. Because of multiple comparisons, the minimum level of significance is $P < .01$

Comparison	χ^2	P
Great Egret vs. Snowy Egret	567.09	<.001
Great Egret vs. Cattle Egret	953.22	<.001
Great Egret vs. Little Blue Heron	531.33	<.001
Great Egret vs. Louisiana Heron	654.82	<.001
Snowy Egret vs. Cattle Egret	41.37	<.001
Snowy Egret vs. Little Blue Heron	32.82	<.005
Snowy Egret vs. Louisiana Heron	34.70	<.001
Cattle Egret vs. Little Blue Heron	34.61	<.001
Cattle Egret vs. Louisiana Heron	35.66	<.001
Little Blue Heron vs. Louisiana Heron	21.18	<.05

found and the distance of nest sites from the edge of the heronry. Higher nests in tall vegetation near the edge of the heronry had higher component scores.

Nest sites of Great Egrets were significantly different from all other species. Great Egrets nested in larger trees, farther from the ground, and in general closer to the edge of the heronry than the other four species. Among the smaller species, nest site differences were not statistically significant.

On the individual variables associated with Component 1, Snowy Egret nests were found significantly closer to the heronry edge that those of Cattle Egrets ($P < .005$). Cattle Egrets nested significantly higher than Louisiana Herons ($P < .005$). Great Egrets differed significantly from all other species on the individual variables.

Component 2: Accessibility.—The variables loading on Component 2 were Transformed Mean Vegetation Openness around Nest, Number of Supporting Branches, and the inverse of the Distance to Nearest Open Space. Nest sites closer to open areas within the heronry had greater lateral openness. Open and more accessible nests might have greater support than less accessible nests because they would be more vulnerable to wind and rain. More accessible nests had higher scores on the component.

Great Egret nest sites were significantly more open and accessible and had greater nest support than did those of the other species. No significant differences were found among the other species.

Great Egrets differed from all the smaller species on all individual variables except Number of Supporting Branches. Although Great Egret nests were supported by more branches, mean differences were significant only for nests of Great Egrets vs. Cattle Egrets ($P < .01$) and Little Blue Herons ($P < .001$). Snowy Egret nests were supported by greater numbers of branches than Little Blue Heron nests ($P < .005$).

Component 3: Protection.—Variables loading on Component 3 were Vegetation Openness above Nest, the inverse of Transformed Mean Vegetation Density around Nest, and the inverse of Transformed above-Nest Vegetation Density. Component 3 describes openness and protection in the immediate vicinity of the nest. The sample space of horizontal and vertical density variables was only 1 m from the center of the nest. The greater the vegetation density above and peripheral to the nest, the lower the reading of openness expected.

Great Egret sites were significantly less protected than were nests of the other species. No significant differences were found on the component for the other species. On the basic variables, Great Egret sites were different from all other

TABLE 6. Comparison of the proportional distribution of species of smaller herons and egrets in sampling quadrats in the Annex–Phillips Island heronry complex, 1974

	Annex		Phillips Island	
Species	Observed	Expected	Observed	Expected
Snowy Egret	40	54.34	23	8.66
Cattle Egret	74	65.55	2	10.45
Little Blue Heron	33	28.46	0	4.54
Louisiana Heron	35	33.64	4	5.36

species. Cattle Egret sites were significantly more open vertically than Louisiana Heron sites ($P < .005$).

Component 4: Shrub/tree-center distance.—Only Distance to Tree Center loaded highly on Component 4. Snowy Egrets nested closer to the center of the tree or shrub than the other species. Among the other species, no differences were found.

A summary of twelve-variable mean vector comparisons among species is presented in Table 5. Minimum level for significance was set at $P < .01$ because of multiple comparisons. Mean vectors of all groups differed significantly, except for vectors of Little Blue Herons and Louisiana Herons which differed only at $P < .05$. Future studies using other variables, however, might show stronger differences between the nest sites of these two species.

PLACE OF OCCUPATION WITHIN THE HERONRY COMPLEX

Great Egrets were found only in quadrats on Phillips Island, although six or seven pairs nested on the Annex in areas other than the study quadrats. Similarly, Little Blue Herons were found only in study quadrats on the Annex, although three or four pairs nested in areas outside the quadrats on Phillips Island.

The presence of mulberry trees on Phillips Island provided a more favorable substrate for Great Egret nests than did the wax myrtle, loblolly pine, and cedars on the Annex. The proportion of birds of the five species nesting on the Annex and Phillips Island differs significantly ($\chi^2 = 151.58$, df = 4, $P < .001$). The difference is not dependent on the distribution of Great Egrets alone because comparison of the distribution of nest sites for only the smaller species of herons and egrets is still significantly different ($\chi^2 = 41.12$, df = 3, $P < .001$). These results are presented in Table 6.

Chi-square one-sample tests were used to determine if the observed numbers of small species nesting on each island were different from those expected (Table 6) on the basis of the proportion of small species nesting on each island. The significance level was set at $P < .01$ because of the number of comparisons being made on the same relationships. Snowy Egrets nested more often than expected on Phillips Island and less often than expected on the Annex ($P < .001$). Cattle Egrets nested more frequently on the Annex and less frequently on Phillips Island than expected. There were no significant differences in the distributions of Little Blue Herons or Louisiana Herons.

Vegetational differences could have been partially responsible for these results. The vegetation on Phillips Island could be unable to support the number of nests found on an equivalent area of the Annex. However, the calculation of expected frequencies for each species is the product of the total number of individuals of that

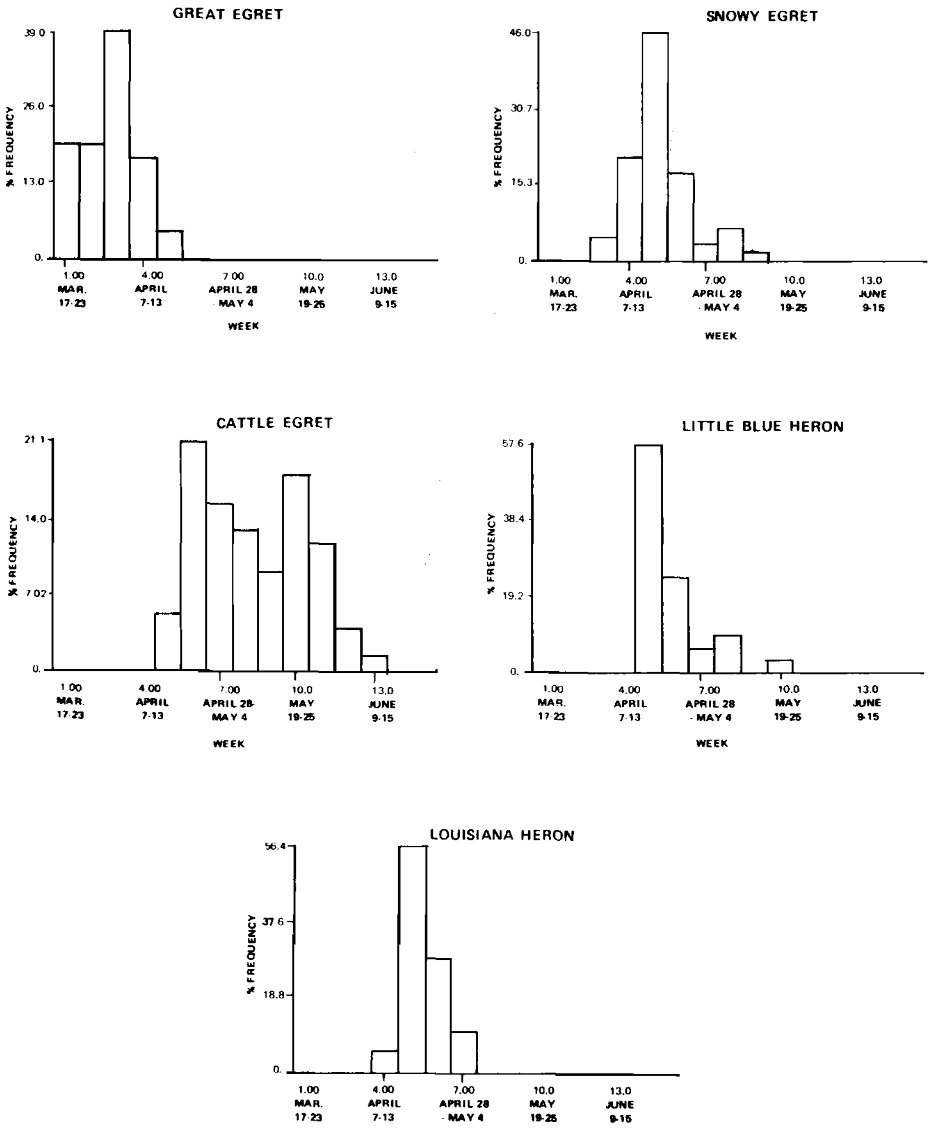

Fig. 2. Frequency distributions of percent of total identified nests of each of five species of herons and egrets identified over the 13-week period spanning 17 March–9 June 1974.

species present on both islands times the proportion of individuals of all small species present on each island. Thus, if the nest-holding capacity of either island is different, this difference will be reflected in the expected frequencies. For example, fewer birds nested on Phillips Island. While the vegetation of Phillips Island may have been partially responsible for the smaller total number of smaller birds nesting on Phillips Island as compared to the Annex, there were more Snowy Egrets found nesting on Phillips Island than expected. Should vegetational differences on Phillips Island be responsible because of a lower nest-holding capacity, fewer birds should have nested there.

TABLE 7. Square-root transformed values of inter-nest distances. The actual among- and within-species inter-nest distance measurements were skewed to the right. To reduce effects of outliers on mean values, distances were square-root transformed

	Inter-nest distances					
	Same species			Other species		
Species	N	$\bar{x}$	SD	N	$\bar{x}$	SD
Great Egret (G)	41	1.30	0.42	25	2.44	1.07
Snowy Egret (S)	62	1.44	0.55	63	1.28	0.38
Cattle Egret (C)	76	1.48	0.65	76	1.09	0.37
Little Blue Heron (B)	33	1.55	0.48	33	1.25	0.39
Louisiana Heron (L)	39	1.86	0.54	39	1.34	0.41

	Intraspecies comparisons (D_{same} vs. D_{other} within each species)		
	t	df	P
Great Egret	5.26	24	<.001
Snowy Egret	1.97	61	>.05
Cattle Egret	6.96	75	<.001
Little Blue Heron	3.44	32	<.005
Louisiana Heron	5.65	38	<.001

On the other hand, Cattle Egrets did nest in significantly smaller numbers than expected on Phillips Island, but probably not because the available nest sites had already been filled by Snowy Egrets or other species. Almost five times as many nests of the smaller herons were found in essentially the same areas on Phillips Island during the 1972 nesting season. Since then, Phillips Island has been suffering a population decline, although the vegetation, and hence the number of available nest sites, has not changed remarkably in the interim. Poor reproductive success in 1972 may have been responsible for the desertion of the colony by adults, which have subsequently not returned to that site for breeding.

TIME OF OCCUPATION OF THE HERONRY

Figure 2 details the percent of total identified nests of each species counted over the period spanning the week of March 17 (Week 1) through the week of June 9 (Week 13). The timing of Great Egret nest building is significantly different from the distribution of all other species (compared by Kolmogorov-Smirnov tests $P < .001$). Cattle Egret nest-building distribution is also significantly different from the distribution of nest building of all other species (all comparisons $P < .001$). Cattle Egrets had a longer distribution in their time of nest building, began building nests later, and had two distinct peaks of nest-building activity.

INTER-NEST DISTANCE

Distances between nests of each species and the nearest nest of the same species or any of the other of the four species were calculated. Those nests that had no nests of the same species or that had no nests of any other species built within the quadrat during the same or previous weeks were excluded from analysis. The distributions of inter-nest distances for all species combined as well as for the individual species over all quadrats were skewed to the right. Square-root transformations were applied.

Great Egrets nested closer to their own species than to any other species (Table 7). Cattle Egrets, Little Blue Herons, and Louisiana Herons nested significantly closer to other species than to their own. Snowy Egrets also nested closer to other species than to each other, although the difference was not significant. These results are those one would expect if in general within quadrats the density of all other species combined is greater than that of any one species. The smaller species of herons did not cluster in significantly homogeneous conspecific groups, but rather were more dispersed within quadrats. Great Egrets did tend to nest in conspecific groups, probably because of the clumped nature of the vegetation meeting their microhabitat nest site requirements.

Discussion

Field ornithologists have long recognized that species select nest sites within certain specific habitats (Lack 1933, Lack and Venables 1939). The assumption was that birds responded to a complex pattern of stimuli rather than to simple variables (Svärdson 1949, James 1971). Principal component analysis summarizes data so that, using clusters of environmental variables, an investigator can describe nest sites with a minimum loss of information. Four dimensions describe the nest sites used by the birds nesting in this heronry complex: vegetation structure, accessibility, protection, and location in relation to the center of the tree or shrub.

Great differences exist between nest sites of Great Egrets and the smaller species. On the first three components, no statistically significant differences were found among mean nest site component scores of any of the smaller species. Snowy Egret nest sites were significantly different from the nest sites of all other species on the component associated with nest location. Principal component analysis does not necessarily maximize differences among groups. Comparisons of mean vectors comprised of all 12 variables show that the nest site microhabitats of all species, except for Little Blue Herons and Louisiana Herons, differ significantly. Studies using variables other than those reported here might show stronger differences between Little Blue and Louisiana Herons.

In some cases, the relationships among species on site variables parallel results found in other studies. Snowy Egret nest sites were found closer to the heronry edge than were those of Cattle Egrets, a result similar to those reported by Jenni (1969) and Meanley (1955). Cattle Egrets may select sites farther from the heronry edge by choice, or they may accept these sites because of their relatively late time of occupation of the heronry. Cattle Egrets built significantly higher and more vertically open nests compared to Louisiana Herons, again possibly a function of their protracted occupation of nest sites. On the other hand, in some years, Jenni reported vertical stratification of nest sites among some of the species he studied. Burger (in press) has also reported some vertical stratification in heronries characterized by relatively homogeneous vegetation. Nest sites in my heronry had considerably more overlap among species. Jenni reported that nest sites of Snowy Egrets were farther out on limbs of trees and shrubs. I found the opposite.

Great Egrets began nesting very early compared to the other species, but this temporal dimension is of limited importance since Great Egrets have been shown to occupy a unique nest site compared to the other species. Snowy Egrets, Little Blue Herons, and Louisiana Herons nested at essentially equivalent times. Cattle Egrets nested later than the other species. Some horizontal partitioning occurred; Snowy Egrets nested in disproportionately large numbers on Phillips Island.

Confirmation of the reliability and validity of differences found in this study will depend on additional careful comparisons of nest site characteristics among different colonies, or over time within the same colony. Herons nest in a broad range of habitats along the east coast of the United States; for example, on the ground or in very low shrubby vegetation as well as in maritime shrub thickets. The differences in the appearance of colonies suggest the potential importance of experience in nest site selection, particularly by offspring that return to the same area to nest. Clearly, long-term studies in the same and different colonies are essential to an understanding of heron nest site selection.

In almost all cases, the combined total of birds of all other species in a quadrat was greater than the total for an individual species. Hence, the determination of the relationship between intra- and interspecific aggression is difficult. The closer nesting of smaller species to species other than their own suggests that nest sites may be chosen as a function of suitable physical characteristics as well as the relative proximity of conspecifics. Possibly conspecifics are avoided. Proof would require equal proportions of all species in the quadrats. The present results do suggest the lack of a general tendency for nesting birds strongly to seek out conspecific clusters among birds which have already selected nest sites. An exception is the Great Egret, which for the most part occupies nest sites that preclude the ability of other species to nest nearby.

Intraspecific aggression generally appeared to be more common than interspecific aggression. Weber (1975) reported similar observations for Cattle Egrets. In New Jersey, Burger (in press) generally found more aggression among species. For herons normally breeding in mixed-species colonies, the amount of time and energy given to nest site selection should be minimized. In the long run, interspecific aggression might be selected against. Vegetation offering a variety of nest site substrates could aid in reducing competition among nesting species. The structurally complex vegetation of my heronry may have allowed nesting species to reduce aggressive competition for nest site resources through complex differential use of environmental variables associated with the site. Less nest site resource diversity in vegetationally simpler colonies such as that reported by Burger may result in more aggressive interaction among species.

All of the species studied occupied territories that, although initially large, compressed during laying and incubation to a very limited area—usually just that immediately surrounding the nest. This characteristic plus a tolerance for the proximity of contraspecifics may allow many birds to occupy a colony over time. This may be the mechanism by which Cattle Egrets occupy a heronry. In my heronry Cattle Egrets began nesting in limited numbers and distributed themselves over time, so that at no time were they in maximum potential competition with other species for nest sites.

This study does not resolve the question of the limit of nest site resources on population size of the various species. Nest site availability and food availability may ultimately act together to determine the size of a population available for breeding and which members of the population actually do breed. But the results of this study do suggest that, within a heronry, each species may be differentially responding to a number of physical, temporal, spatial and possibly social variables, permitting a number of different species to occupy a colony for nesting.

The geographical area encompassed by this study was very small as was the number of species and numbers of nest sites of each species. The range of types of habitat is not broad. Definitions of kinds of stimulus variables of importance for other animals is always troublesome. Moreover, measurement of these stimuli is difficult and subject to error, especially in field settings such as that described here. Future studies should include: (1) analysis of nest site characteristics of the species in as wide a geographical area and in as diverse a number of habitats as possible; (2) incorporation of new variables into studies of nest site selection in addition to those described in this study; (3) exploration of long-term stability of numbers of breeding birds of the species nesting in colonies to determine equilibria between species nesting within an area; and (4) investigation of site tenacity and differential return to geographical areas for young and adults of various species.

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APPENDIX

Description of Methods of Measurement:

1. *Nest height above the ground*.—The distance from the bottom of the nest to the floor of the heronry was measured to the nearest 0.1 m.

2. *Height of vegetation at the nest*.—The distance from the top of the vegetation immediately above the nest to the floor of the heronry was measured to the nearest 0.1 m.

3. *Vegetation openness above the nest* . —The intensity of light penetrating the vegetation as compared with the intensity of light in open unobstructed sky was expressed in percent and measured with a device modified from a design of Horn (1971) held vertically above the nest. The less vegetation above the nest, the greater relative light intensity and the greater the reading. This measure is related to, but is not the exact complement of, cover. A greater area (70° angle subtended) than that immediately above the nest was measured, since it was assumed that the birds would respond to an area greater than the exact diameter of the nest. The readings using this device were reliable, but in a few very open areas on very bright sunny days, reflected light and light coming in through very thin leaves resulted in some increase in readings. The device was recalibrated for maximum intensity of open unobstructed sky at least every 30 min, often more frequently.

4. *Mean vegetation openness around nest*.—The same device described above was used to determine the mean horizontal relative light intensity values of three points 120° apart trisecting the vegetation concentric to the circumference of the nest. The direction in compass degrees of the first of these three points was determined from a random numbers table.

5. *Mean vegetation density 1 m around the nest*.—The mean number of contacts of leaves, twigs, or branches of vegetation with a meter stick held horizontally from the center of the nest at each of three points trisecting the vegetation concentric to the circumference of the nest. The points were the same as those for mean vegetation openness around the nest.

6. *Vegetation density 1 m above the nest*.—The number of contacts of leaves, twigs, or branches of vegetation on a meter stick held vertically above the center of the floor of the nest.

7. *Diameter of the nest branch*.—The diameter of the main branch supporting the nest (cm). In the case of a nest resting in the fork of two branches, the diameter of the branch at the intersection of the forks was taken.

8. *Diameter of the nest tree*.—The diameter of the tree or main shrub stem supporting the nest at the height of 1 m above the heronry floor.

9. *Distance of nest from tree or shrub center*.—The distance of the nest to the trunk of the tree supporting the nest to the nearest 0.1 m. This measure was straightforward for species such as loblolly pine, white mulberry, and paper mulberry, whose configurations are unusually tree-like, with a trunk and with crown branches extending laterally. In shrubby vegetation, the variable was evaluated as the distance of the nest from the "apparent center" of the shrub holding the nest.

10. *Number of branches supporting the nest*.—The total number of branches supporting the framework of the nest.

11. *Distance of nest to nearest open space within heronry vegetation*.—Primarily defined in relation to the more shrubby vegetation within the heronry. In many areas of the heronry the shrubby vegetation would suddenly open up in places or become very thin and low, usually exposing the floor of the heronry. These open spaces appeared to permit the birds ready access to nests located deep within the vegetation of the heronry. The measured distance was the distance, to the nearest 0.1 m, from the coordinates of location of the nest to the center of the nearest open space within the shrubby vegetation of the heronry.

12. *Distance of nest to heronry edge*.—Measured with the use of coordinates for the location of each nest, this was the distance, to the nearest 0.1 m, of the nest to the nearest edge or limit of the major body of the vegetation of the heronry.