

FEEDING HABITATS OF NESTING WADING BIRDS: SPATIAL USE AND SOCIAL INFLUENCES

R. MICHAEL ERWIN

*Migratory Nongame Bird Section, Patuxent Wildlife Research Center,
U.S. Fish and Wildlife Service, Laurel, Maryland 20708 USA*

ABSTRACT.—In an effort to relate social interactions to feeding-habitat use, I observed six species of wading birds near a major colony site in coastal North Carolina. Three spatial scales of habitat use were considered: the general orientation to and from the colony (coarsest level), the habitat "patch," and (at the finest level) the microhabitat. Departure-arrival directions of Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Cattle Egrets (*Bubulcus ibis*), Little Blue Herons (*Egretta caerulea*), Tricolored Herons (*Egretta tricolor*), and Glossy Ibises (*Plegadis falcinellus*) were monitored at the colony site to document coarse patterns of feeding-habitat use. Added to these data were observations made at five different wetland sites to monitor between-habitat and within-habitat patterns for the five aquatic-feeding species.

The results indicated a broad and variable use of feeding habitat over time. At the coarsest scale (i.e. orientation at the colony), diffuse patterns, influenced little by either inter- or intraspecific social interaction, were found for all species. At the next level (habitat "patch"), only one of five wetland sites was relatively consistent in attracting feeding birds, and its use increased from May to June. Few groups were seen at four of the five sites. At the one "attractive" site, the within-habitat patterns again were spatially variable over time, except for those of the abundant Snowy Egret, whose microhabitat preference was fairly consistent. Glossy Ibises and Snowy Egrets frequently formed mixed-species groups, Little Blue Herons were the least social, and Great Egrets and Tricolored Herons generally occurred in groups of less than 10 birds but rarely in groups larger than 30. The close association between Snowy Egrets and Glossy Ibises appeared to be based on a "beater-follower" relationship, wherein the probing, nonvisually feeding ibises make prey more available to the followers. In the study area, local enhancement appeared to play a more important role than did any "information-sharing" at the colony. Received 15 July 1982, resubmitted 6 December 1982, accepted 11 April 1983.

THE question of how animals use their foraging area has been a central theme in behavioral ecology (Brown and Orians 1970, Schoener 1971, Orians and Pearson 1979, Morse 1980). As in many areas of ecology, however, information generated from empirical studies has lagged behind theoretical constructs of what animals "ought" to do. Optimal-foraging theory makes a number of predictions about the use of space or patches over time, but most tests of the theory have been under laboratory conditions. Little attempt has been made to understand how "central-place foragers" (Orians and Pearson 1979) make hierarchical decisions relative to the spatial scale of the foraging mosaic (Morse and Fritz 1982). For colonially nesting birds, for instance, the first "decision," the general direction to take from the central place (colony), is made at a coarse scale; at the next level, a specific habitat type, e.g. pond, marsh

edge, tidal flat, is selected; finally, at the finest level, choice of microhabitat is made.

Recently, avian ecologists have shown increasing interest in social influences upon feeding-habitat use (Crook 1965, Ward 1965, Horn 1968, Morse 1970, Kushlan 1978a; see Morse 1980 and Wittenberger 1981 for reviews). Many students of social feeding in waterbirds have focused on testing Ward and Zahavi's (1973) information-center hypothesis (Krebs 1974; Erwin 1977, 1978; Ogden 1978; Custer and Osborn 1978; Pratt 1980; Bayer 1981, 1982; Evans 1982; Waltz 1982). This hypothesis states that social groups such as breeding colonies provide important food-location information whereby unsuccessful foragers cue on successful birds, following them to "better" feeding sites.

The objectives of this paper are twofold: (1) to examine how several wading-bird species use

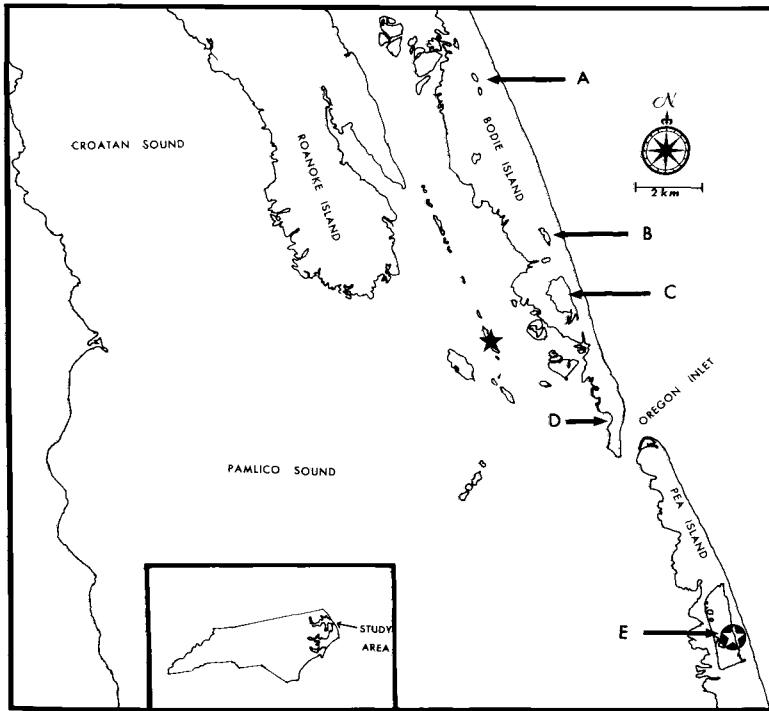


Fig. 1. The study area showing locations of the feeding sites (A-E), the major study colony (solid star), and the small colony at Pea Island (enclosed star).

their feeding environment at three spatial scales over time, and (2) to document whether or not social interactions, both in the vicinity of the colony and at the feeding ground, are important influences on feeding-habitat use. The results of this study, based upon mixed-species assemblages of wading birds, may then be applied to other animals confronted with a complex mosaic of feeding habitat that varies over time and in space.

METHODS

During late May and June 1979 and May 1980, I observed Cattle Egrets (*Bubulcus ibis*), Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Little Blue Herons (*Egretta caerulea*), Tricolored Herons (*Egretta tricolor*), and Glossy Ibises (*Plegadis falcinellus*) at a coastal area (Fig. 1) in North Carolina. Nest counts were made at the major study site (Fig. 1, site 03-05 in Parnell and Soots 1979; site 500002 in Osborn and Custer 1978) in late May and again in mid-June.

Flight directions at the colony.—Data were collected on flight directions taken by birds going to and from the colony to assess patterns of spatial use at the

grossest scale. From two to four observers stationed around the perimeter of the colony counted all departing and arriving birds for 1-h periods on 6 days in June 1979. Standardized forms were used to record the species, "activity" (departure or arrival), size and composition of any group flights, direction used, time, and wind direction and speed. A group was defined as two or more birds that flew in the same direction for at least 200 m within approximately 50 m of each other. The counts were made during mid-afternoon at low tides from 8 to 19 June when the majority of birds were feeding young.

The direction used by each bird in flight was tallied as falling into one of eight 45° sectors of a circle, with the colony center being the center. Individuals were observed for at least 100 m before their true course was recorded, because some birds changed course from their initial heading. Two assumptions were made concerning flight directions: (1) flights were only between feeding locations and the nesting colony, with no other activities [e.g. travel to drinking sites (Pratt 1977)] adding "noise," and (2) birds flew directly from the colony to the feeding site. The assumptions are important to the premise that initial (or final) flight direction reflects the location where the individuals feed. Because most of the nests of all

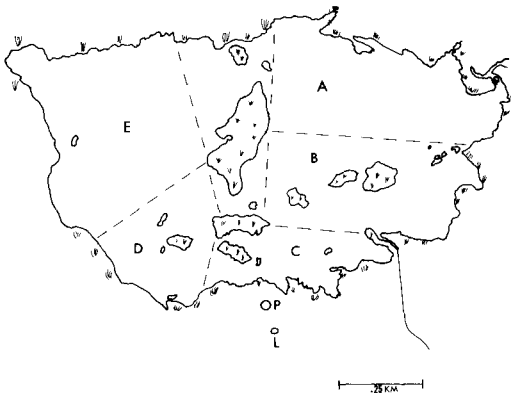


Fig. 2. Site C, Bodie Island Light marsh pool, showing five feeding zones, A-E. Observations were made from an elevated observation platform (OP) just east of the lighthouse (L). The unlettered middle zone was obscured from view by vegetation.

species had young, feeding demands on parents were at a maximum (Bateman 1970, Erwin and Ogden 1980); therefore, the first assumption seems reasonable. Further, Bateman (1970) showed that in his three-species sample of telemetered wading birds, all flights were made between the colony and feeding sites when young were being fed in the colony. The second assumption is verified by Bateman's (1970) and Custer and Osborn's (1978) reports that, birds "generally flew directly" to the landing (= feeding) site.

Statistical analyses were based upon nonparametric measures (Siegel 1956) and circular statistics (Batschelet 1972, 1981; Moore 1980). To calculate daily direction vectors for each species, I used the midpoints of each 45° sector. The resultant vector values, r , were calculated for each day; then, a composite vector was calculated based on all observations over n days. The length of the vectors ($r_{max} = 1.0$) reflects the degree of variability in the use of that direction. A low r value reflects high variability and vice versa (Batschelet 1972). Raleigh tests (Batschelet 1972) were used to test for differences in directionality over time and between species.

Feeding-site use away from the colony.—Five feeding areas (see Fig. 1) were monitored near the nesting colony, the choice of sites based on ease of investigator access. Site A (Fig. 1) was a small borrow pit along the road. Site B was a natural, high-marsh, brackish pool. Site C, also a high-marsh area, had a dam and spillway outlet, allowing water regulation. These sites were slightly brackish and very shallow (≤ 1 m average depth), with water levels varying somewhat during the study period. Site D was an approximately 1.5-km expanse (ca. 40 ha) of *Spartina* salt marsh and mud-flat area beneath the Oregon Inlet bridge, from which observations were made. Site

TABLE 1. Summary of daily flight vectors of birds from the heronry.^a

Species ^b	Number nests estimated	Number flights	Orientation statistics		
			Daily mean r^c	Range	Composite r^d
GREG	114	255	0.33	0.23–0.49	0.26
SNEG	120	284	0.36	0.28–0.55	0.30
CAEG	66	148	0.42	0.13–0.87	0.32
LBHE	90	189	0.50	0.32–0.92	0.40
TRHE	108	228	0.29	0.02–0.76	0.22
GLIB	96	186	0.51	0.25–0.64	0.33

^a Data from 6 days in June 1979.

^b Species abbreviations: CAEG = Cattle Egret; GLIB = Glossy Ibis; GREG = Great Egret; LBHE = Little Blue Heron; SNEG = Snowy Egret; TRHE = Tricolored Heron.

^c The average for all days, unweighted for sample size.

^d Based upon total observations over n days.

E was a fresh-brackish impoundment located at the north end of Pea Island National Wildlife Refuge. Only at Site D were minor daily fluctuations in water level observed, the result of tides and, more important, wind (J. Parnell pers. comm.). Tidal fluctuations were small in this region (mean amplitude < 0.5 m, U.S. Dept. Commerce 1978).

From 0900 to 1500, I observed feeding wading birds at the five sites, with approximately 0.5–1.5 h spent per site. Visual sweeps of each site were made with binoculars and spotting scope, and the total number of each species was recorded. At Site C, data on "within-habitat" use were collected by dividing the marsh into five feeding zones (Fig. 2). The presence and location of each individual and groups of birds were noted. A group was defined as adjacent birds being 5 m or less from each other. Distances were determined by estimating the number of "bird lengths" between individuals (small herons, ibis, Snowy Egret = 0.5 m, Great Egret ≈ 1 m).

RESULTS

Flight directions at the colony.—Resultant vectors showing the mean daily feeding-flight directions were calculated for all species in the colony (Table 1, Fig. 3). The patterns revealed by all the species show wide use of many foraging areas, both on any given day and over a series of days. Five of the six species used an average of seven of the eight sectors per observation-day. Cattle Egrets averaged about five sectors per observation-day. Composite values (Table 1) yielded z values (Raleigh test) that were significant ($P < 0.01$) for all species, indicating a nonuniform distribution.

All six species used feeding areas primarily

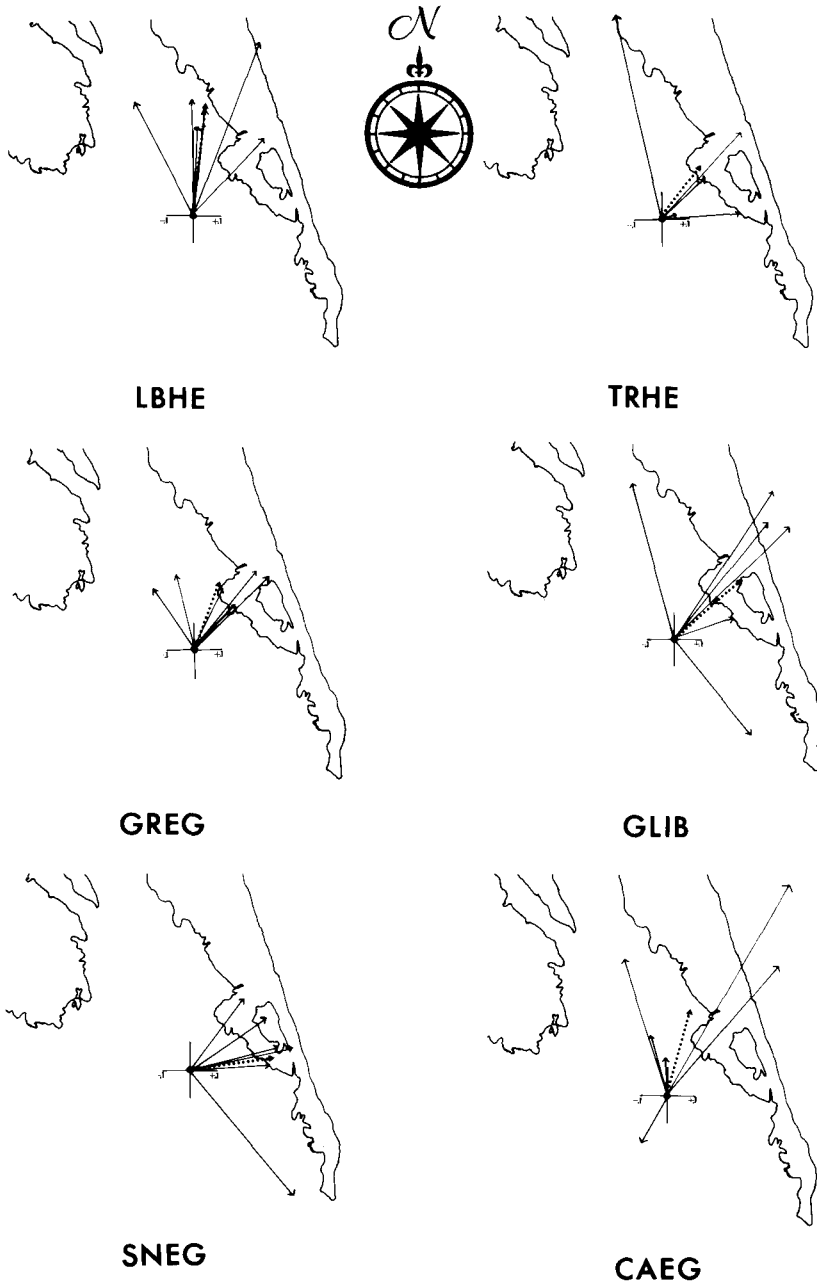


Fig. 3. Resultant vectors of daily feeding flights by six wading bird species at Oregon Inlet. Species abbreviations as in Table 1. Length of arrows varies *inversely* with degree of variation for each day; arrows do *not* show feeding-site locations. The overlay map is presented to show only major features around the colony sites. The dotted arrow indicates the composite (overall) r (see Table 1). A scale ($r = -0.1$ to $+0.1$) is shown on the x-axis to assess the magnitude of the arrows.

TABLE 2. Relative participation in group flights to and from the herony, 1979.

Species ^a	Total number birds observed	Percentage of birds in groups ^b		Total percentage of birds in groups
		Arriving	Departing	
GREG	310	2.3 (3)	1.7 (3)	4
SNEG	325	4.3 (6)	3.7 (6)	8
CAEG	167	7.0 (6)	7.0 (6)	14
LBHE	229	2.5 (3)	2.5 (3)	5
TRHE	277	3.6 (5)	1.4 (2)	5
GLIB	248	16.9 (14)	10.9 (8)	28

^a Species abbreviations as in Table 1.

^b Number of groups in parentheses.

to the east and north of the colony, where there were brackish marshes and impoundments. The only anomaly was one day on which Cattle Egrets flew across Pamlico Sound, probably to feed in plowed fields on the mainland (Custer and Osborn 1978). This mean direction would require a one-way flight of at least 8 km, similar to distances reported by Bateman (1970, 10.6 km) and Custer and Osborn (5.7 km).

To compare how within-day variation in directionality contributed to among-day, or overall, variation, I derived both daily mean vectors and composite vectors for each species (Table 1). For example, a certain species may use a wide variety of sites over a series of days (low composite r value) but, on each day, may be highly directional, yielding a high daily mean r . This result would be expected for species that forage in large groups (Krebs 1974, Kushlan 1978a). There was large difference in r values only for the Glossy Ibis. For the other species,

the differences between daily and composite r values were small.

To test whether or not flight directions used on a given day were dependent on the direction taken on other days, I calculated a Kendall's Coefficient of Concordance, W (Siegel 1956) for each species over a sequence of days. This nonparametric procedure requires that categories (sectors) be ranked according to the relative counts per sector. For all species, the W statistic yielded significant χ^2 values. The test values were as follows: $W = 0.65$ (GREG), $P < 0.01$; $W = 0.63$ (LBHE), $P < 0.01$; $W = 0.76$ (SNEG), $P < 0.01$; $W = 0.60$ (CAEG), $P < 0.01$; $W = 0.63$ (TRHE), $P < 0.01$; and $W = 0.56$ (GLIB), $P < 0.01$. The data were corrected for ties for all species. Thus, daily directions showed some pattern for all species and were not random across days.

Because the species studied often feed in mixed-species aggregations (Willard 1977, Kushlan 1978a, see below), I tested for a social influence using a modified Raleigh Test (Moore 1980). I tested the null hypothesis that there was no difference in the directions taken by the two species compared. All pairwise comparisons (15 for six species) were made for each of the species pairs. In all comparisons, the resultant difference vector was insufficient to reject the null hypothesis. The high variation with each species may mask any differences between species.

The social influence was also examined by monitoring the frequency of all group flights to and from the colony. Only Glossy Ibises, and to a lesser extent Cattle Egrets, flew in groups with any regularity (Table 2). No interspecific flocks were seen. If the colony is acting as an

TABLE 3. Daily variability in use of selected feeding sites by wading birds, 1979.

Location ^a	Number days	Number of individuals				
		Max.	Min.	\bar{x}	1 SD	C.V. ^b
North Pond (A)	11	12	1	3.9	3.2	82
Observation Post 8 (B)	6	8	1	2.7	2.7	100
Bodie Island Light (C) ^c	13	245	10	94.9	88.4	93
May	6	40	10	20.2	15.0	75
June	7	245	119	178.7	53.8	30
Oregon Inlet (D)	7	23	0	8.3	7.7	93
Pea Island (E)	9	18	2	8.3	5.0	60

^a The name of the location is followed by the letter designation in Fig. 1. Locations A, B, C, and E are shallow fresh-brackish marsh pools.

^b Coefficient of variation = $(1 \text{ SD})/\bar{x} \times 100$

^c Only at this site were numbers sufficient to compare May and June results.

TABLE 4. Summary of Kendall's Rank Tests of Concordance^a of use of feeding zones^b by wading birds at Bodie Island lighthouse marsh.

Comparisons	Period	<i>n</i> (days)	<i>n</i> (individuals)	<i>W</i> ^c value	<i>P</i> level
All species	May 79	3	90	0.13	ns
	June 79	7	1,092	0.37	<0.05
	May 80	5	86	0.34	ns
	Overall	15	1,268	0.04	ns
Snowy Egret ^d	June 79	6	358	0.56	<0.01
	May 80	4	63	0.53	ns
	Overall	10	475	0.41	<0.01
Tricolored Heron	June 79	5	222	0.34	ns

^a Tests the null hypothesis that the ranks of zone are independent over a series of days.

^b Feeding zones A-E, Fig. 2.

^c *W* value is the test statistic from the Kendall Rank Test.

^d The numbers I saw on most of the 7 days in May 1979 were insufficient to allow me to conduct rank tests.

"information center," the frequency of birds departing from the colony in groups should greatly exceed group-arrival frequencies. Binomial tests showed no significant differences between the tendency for birds to depart in groups and to arrive in groups [$P = 0.14$ (GLIB), $P = 0.23$ (TRHE), $P > 0.60$ (others)]. Group sizes were usually very small, 2-3 birds, but on five occasions, Glossy Ibises traveled in flocks of 5-8 birds. The largest group in which any of the other species was observed flying was three (two cases in Snowy Egrets, one in Great Egrets).

Feeding habitat use.—Only one of the five study plots, Site C, attracted large numbers of wading birds (Table 3). Despite the fact that a small colony (about 250 pairs of the six species) nested at the Pea Island Impoundment in 1979, only small numbers fed there. Sites A and B had the lowest use in 1979. At North Pond (A), at least one Great Egret was present on 9 of 11 days in 1979 and 3 of 4 days in 1980. Use of the same

area of the pond by the egret(s) suggested that perhaps the area was a feeding territory (Custer and Osborn 1978, Bayer 1978).

Despite moderate (± 0.5 m) changes in water levels in the intertidal flat area, the variability of use (C.V.) of the inlet area was similar to that in the impoundments. Only Site C had regular (low C.V.) use and only in June, when nesting food demands were at their peak.

At the "within-habitat" scale (Fig. 2), the use of feeding zones within Site C changed on both a short-term (daily) and long-term (month, year) basis. To test whether or not species were consistent in their relative "preference" of areas (ranked by abundance), I conducted Kendall Rank Tests of Concordance, first for all species, then for the Snowy Egret, the most abundant species (Table 4). For all species combined, in both years, there was no indication that certain zones were strongly preferred over a series of days ($W = 0.04$, $P > 0.05$). Snowy Egrets, how-

TABLE 5. Size distribution of feeding groups^a at several feeding sites, 1979-1980.

Species ^b	Size of group						Means	
	1	2-5	6-10	11-20	21-30	>30	Group ^c	Overall
GREG	39	8	5	0	0	1	5.3	2.4
SNEG	99	34	14	5	2	5	8.8	3.8
LBHE	20	11	1	0	0	0	3.2	1.7
TRHE	69	33	6	4	0	0	4.8	2.4
GLIB	26	34	9	2	1	6	11.5	7.8

^a Groups composed of individuals 5 m or less from their nearest neighbor.

^b Abbreviations as in Table 1.

^c Mean group size for all groups of two or more.

TABLE 6. Composition of groups of feeding wading birds at Bodie Island lighthouse marsh, 1979.

Species ^a	Group ^b									Number of individuals
	Small (3-10)			Medium (11-30)			Large (>30)			
	Mono (n)	Mixed (n)	Percentage	Mono (n)	Mixed (n)	Percentage	Mono (n)	Mixed (n)	Percentage	
GREG	1	5	34	0	4	27	0	2	<1	38
SNEG	10	17	55	1	11	42	0	8	39	450
LBHE	1	5	30	0	2	21	0	1	<1	29
TRHE	8	17	41	0	9	33	0	7	11	195
GLIB	2	4	45	0	7	34	0	8	53	410

$$\chi^2 = 237, df = 8, P < 0.001^c$$

^a Abbreviations as in Table 1.

^b The number of monospecific and mixed groups are indicated for each species in each of three size classes, with the overall percentage composition of each species in each mixed-group category.

^c A 5 × 3 Chi-square contingency analysis based on number of individuals of each species in the three size classes.

ever, did show some preference. Even though numbers were small in May 1979, there appeared to be little year-to-year correspondence in zone "preference" of Snowy Egrets. On 7 days in May 1979, zones E (3 days) and B (2 days) had the highest numbers, whereas in 1980, zone E ranked first only once and zone B never over 5 days.

At Site C, there was a marked seasonal-use component. The mean number of Snowy Egrets in May in both 1979 and 1980 was only 12.3 birds, but, in June 1979, the mean increased to 55.7 birds. This increase may have been caused by increased food demands of nestlings (above), by changing prey conditions, or both. The consistency of use in May between years was somewhat unexpected because of lower water levels in 1980.

Feeding associates.—At all locations in 1979 and 1980, Glossy Ibises fed in close proximity to one another more often than did the other species; Snowy Egrets ranked second and Little

Blue Herons last in group feeding. Great Egrets and Tricolored Herons were intermediate and very similar (Table 5).

Group sizes ranged from 3 to 150 in 65 groups analyzed at the Bodie Island lighthouse marsh pool (Site C). Only rarely were small groups (2-5 birds) seen at the other four sites. The individual species were not equally distributed among three group-size classes (Table 6). Contingency table analyses showed that Glossy Ibises occur more often than expected in larger groups, whereas Great Egrets, Little Blue Herons, and, to a lesser extent, Tricolored Herons are overrepresented in small groups. Glossy Ibises and Snowy Egrets are the predominant members across the three size classes. Great Egrets and Little Blue Herons show the greatest proportional decrease in the larger groups. Tricolored Herons and Snowy Egrets form small monospecific groups most frequently; a larger monospecific group was documented only once (Snowy Egrets).

TABLE 7. Analysis of intraspecific and interspecific crowding for five wading birds.

Encountering species	Numbers ^a encountered of						Total	P.I.E. ^b
	SNEG	TRHE	LBHE	GREG	GLIB			
SNEG	10.3 ± 13.5	5.2 ± 5.1	2.3 ± 1.9	2.9 ± 2.4	24.4 ± 26.6	45.1	0.77	
TRHE	11.6 ± 15.7	5.6 ± 4.3	2.6 ± 1.6	3.0 ± 2.3	20.5 ± 24.1	43.3	0.87	
LBHE	15.0 ± 24.1	5.0 ± 4.8	3.9 ± 2.3	2.5 ± 0.7	28.0 ± 41.6	54.4	0.93	
GREG	15.5 ± 21.2	7.0 ± 7.0	5.0 ± 0	3.9 ± 2.0	33.7 ± 33.2	65.1	0.94	
GLIB	19.2 ± 19.4	7.1 ± 5.9	2.7 ± 2.1	1.3 ± 0.6	20.5 ± 25.1	50.8	0.60	

^a Numbers are the average (± 1 SD) densities (numbers of individuals in same group) of species Y encountered by individuals of species X.

^b Probability of interspecific encounter (proportion) (after Hurlbert and Keith 1979).

TABLE 8. Species abundance and group association in mixed-species feeding groups, Bodie Island lighthouse marsh, 1979.

Focal species	Number of groups		Rank of species associated ^a				
			GREG	SNEG	LGHE	TRHE	GLIB
SNEG	46	Rank (percentage of groups)	3		4	1	2
		Rank (abundance) ^b	2		4	1	3
GLIB	21	Rank (percentage of groups)	3	1	4	2	
		Rank (abundance)	3	2	4	1	

^a Abbreviations as in Table 1. Ranks based on relative frequency of group association.

^b Based on counts made at the study colony and at the Pea Island Impoundment colony (Parnell and Soots 1979) to determine regional populations.

A convenient method for expressing both interspecific and intraspecific crowding conditions is to generate a matrix for encounter frequencies (Hurlbert and Keith 1979). Table 7 indicates the relative degree of both intraspecific (principal diagonal) and interspecific (off-diagonal) crowding. Intraspecific crowding was highest for Glossy Ibises, while their interspecific crowding (P.I.E. = 0.6) was lowest of all the species. Snowy Egrets formed relatively dense groups with other Snowy Egrets and also with ibises. The other three species formed small intraspecific assemblages (3-6 birds on the average) but encountered dense numbers of Glossy Ibises and Snowy Egrets in the relatively small number of cases in which the latter species occurred.

The association among species pairs can also be examined by comparing the frequency of association of species and their abundances (Waser 1982): for the null model, a given species *A* has an expected probability of associating with species *B* of $P_{A \cdot B} = \frac{N_B}{N_T}$ or, simply, the abundance of species *B* (N_B) relative to the numbers of all species that might also be associated (N_T). Rank abundances and the percentages of groups with associated species pairs are shown for the two abundant species in Table 8. The only species that associates with another more often than predicted by their relative abundances is the Snowy Egret with the Glossy Ibis. In the larger groups (≥ 30), both species occurred in all cases, with Glossy Ibises outnumbering the egrets in six of eight cases.

The degree to which social foraging is related to group-flight tendencies can be shown by referring to Tables 2 and 5. Of the five aquatic

feeders, Glossy Ibises show both a strong tendency to forage together and to fly to and from the colony together (ranked first for both). Snowy Egrets show a similar pattern, ranking second in both. Thus, the tendency to feed in groups appears to be coupled to group-flight behavior near the nesting colony.

DISCUSSION

Spatial use.—At all three spatial scales considered, i.e. at the colony, habitat, and microhabitat levels, wading birds seemed to be highly variable in their spatial and temporal use of their feeding environment. Individuals left the colony, usually as single birds, heading in a variety of directions, with the mean direction often changing considerably from day to day. The choice of habitat varied, probably depending upon water levels, types of prey, and previous experience in certain areas (Royama 1970). Only one site (C) seems to be a "hot spot" (Pleasants and Zimmerman 1979), but, even here, use was high only in June. At the finest level, i.e. within-habitat, significant daily changes in relative numbers per zone occurred. Snowy Egrets did show some consistency over the short term, however.

The high degree of variability shown in space and time by wading birds probably reflects the unpredictable nature of their mobile, patchy prey resources (Krebs 1974, Kushlan 1978a, 1981). Some mechanisms that birds may use to mitigate this uncertainty are discussed below.

Information-center.—The critical element of the information center hypothesis (ICH) is a demonstration that birds follow other birds from colonies or roosts to prospective feeding

sites (Ward and Zahavi 1973, Bayer 1982). My results suggest that such a mechanism may not be widespread, because only Glossy Ibises and Cattle Egrets frequently flew in groups, and groups of *arriving* birds were as common as departing groups. Bayer (1982, Table 1) noted that arrival at the colony in groups is fairly common in many colonial birds and that group departures could be a statistical artifact of grouped arrivals, unrelated to any social mechanism. Alternatively, group flights might enhance food location via local enhancement, not through any information exchange at the colony (Evans 1982).

Failure to record frequent departing groups of Cattle Egrets is surprising in light of a number of other studies of this species that have documented flocking (Bateman 1970, Siegfried 1971, Custer and Osborn 1978). In Florida, both Snowy Egrets and, to a lesser extent, Tricolored Herons were frequently (29% and 15%, respectively) seen departing in groups at one colony (Ogden 1978). Perhaps observations made at other times, such as early morning, might have yielded somewhat different results. In Florida (J. Ogden pers. comm.) and southern North Carolina (T. Custer pers. comm.), early large-scale departures occur for several species at mixed colonies, possible because of the attendance at the colony of large numbers of non-breeding birds. Perhaps the initial departure from the colony on each day is the critical one for which directional information is important (T. Custer pers. comm.). In addition to examining time influences, researchers should study colonies in areas with significant tidal fluctuations, because at high tide fewer areas are available for feeding (Custer and Osborn 1978) and the degree to which information exchange is necessary thus is influenced.

Local enhancement.—Following individuals from the colony to locate good feeding areas (ICH) may not be necessary in many situations where the feeding universe is already restricted (see Krebs 1974, Des Granges 1979, Pratt 1980). Under these circumstances, individuals may simply commute between the colony and a certain region (e.g. northeast quadrat in Fig. 3), selecting the specific habitat and microhabitats by means of proximate cues such as local enhancement (Turner 1964, Krebs 1974), water level, etc. Cueing on the presence of other feeding individuals, either conspecific or het-

erospecific, appears to be an effective mechanism for reducing uncertainty (Ward 1965; Krebs 1974; Kushlan 1977, 1978a; Caldwell 1981). A number of waterbird studies indicate that certain core species seem to attract others; Snowy Egrets in tropical flocks (Caldwell 1979, 1981), White Ibis (*Eudocimus albus*) in Florida (Kushlan 1978b), and Roseate Spoonbills (*Ajaia ajaja*; Russell 1978) appear to attract at least one other species to them. Willard (1977) noted that Snowy Egrets and Glossy Ibises were usually central species in mixed aggregations. The role of ibises and spoonbills appears to be that of "beater," whereby the action of the beater birds makes food more available to the "follower" species (Christman 1957, Parks and Bressler 1963, Russell 1978). In this study, Glossy Ibises appeared to perform a "beater" role, similar to that of the related White Ibis in Florida.

Snowy Egrets alone may also attract other waders (Caldwell 1981), but, because there were no large (>30) monospecific groups of Snowy Egrets in my area, I could not examine this more thoroughly. Only one of four groups in the 20–30 size class had Snowy Egrets but no ibises. Group attendance does not appear to be uniformly attractive to all species, at least across all group sizes. Even though Snowy Egrets and Glossy Ibises are well represented across the three group sizes (Table 6), Great Egrets and Little Blue Herons are not common in large groups. Interestingly, both species are relatively slow and methodical in their feeding method. In larger groups, the confusion and interference of other species may disrupt the foraging of these two species (Royama 1970, Kushlan 1978a). Thus, species that are either nonvisual (ibis) or highly plastic (Snowy Egrets) in their feeding repertoire seem to favor large aggregations.

The fact that Glossy Ibises fly in groups, feed socially in both single- and mixed-species aggregations, and may often be the "core species" in such groups seems counter-intuitive for such dark, cryptically colored species (Kushlan 1978a). Studies have shown that white birds or models are more attractive to other waders than dark birds (Kushlan 1977, Caldwell 1981), but some dark species also have been shown to be "attractors" (e.g. Krebs 1974). The generality of the plumage color-gregariousness relationship may need further investigation and refinement.

ACKNOWLEDGMENTS

I thank C. Deutsch for assistance in the fieldwork. The staff at Pea Island National Wildlife Refuge granted me access to their property. D. Brown and B. Dowell provided technical and statistical support. K. Hall typed the manuscript. Drafts of the manuscript were improved by the comments of R. Bayer, C. Bunck, T. Custer, W. Dryer, M. Fuller, D. Mock, J. Wiens, B. K. Williams, and an anonymous reviewer, to all of whom I am grateful.

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