

FEEDING HABITAT USE BY COLONIALY-BREEDING HERONS, EGRETS, AND IBISES IN NORTH CAROLINA

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ABSTRACT.—Nine species of herons, egrets, and ibises were followed by airplane from a nesting colony near Beaufort, North Carolina to their feeding sites. Except for Cattle Egrets, which flew exclusively to fields and dumps, the birds flew mainly to saltmarsh habitat. The selection of feeding habitats by Great Egrets and Louisiana Herons was directly related to tidal depth. The Great Egret was the only species that effectively used eelgrass beds, and its use of this habitat was restricted to between 1.5 h before and after low tide. We suspect that shorter-legged herons did not use eelgrass regularly because the water was too deep.

Most Great Egrets, White Ibises, Louisiana Herons, and Snowy Egrets used areas near the colony (<4 km). Great Egrets, Black-crowned Night Herons, and White Ibises flew farther from the colony at high than at low tide. Great Egrets traveled farther from the colony when they used thermals; rate of travel to feeding sites was the same, however, whether or not they used thermals.

Aggressive encounters were observed at the landing sites of Great Egrets, Louisiana Herons, Snowy Egrets, and Black-crowned Night Herons. In contrast to the other species studied, Cattle Egrets and White Ibises often flew in groups to feeding sites. Indirect evidence supports the hypothesis that colonies can act as "information centres," wherein unsuccessful birds follow successful ones to better feeding locations. *Received 31 January 1978, accepted 7 May 1978.*

THE use of wetland habitats by herons, egrets, and ibises (here collectively termed herons) is not well known. Jenni (1969) found that Snowy Egrets (*Egretta thula*) feed in open areas, Little Blue Herons (*Florida caerulea*) in heavily vegetated areas, and Louisiana herons (*Hydranassa tricolor*) along banks or floating vegetation where the water level drops rapidly. Kushlan and Kushlan (1975) described the feeding habitat preferences of the White Ibis (*Eudocimus albus*) in southern Florida, and Meyerriecks (1962), Kushlan (1976a), and Custer and Osborn (1978) found that longer-legged herons feed in deeper water than shorter-legged ones.

The distance herons travel from a colony to feeding sites is also poorly understood. Published estimates of the maximum distance (km) for various species are as follows: Cattle egret (*Bulbulcus ibis*) 28.5 (Bateman 1970), 25.8 (Hopkins and Murton 1969), 19.3 (Craufurd 1966, Skead 1966), and 29 (Siegfried 1971); Roseate Spoonbill (*Ajaia ajaja*) and Grey Heron (*Ardea cinerea*) 32.2 (Beetham 1910) and 19.3 (Nicholson 1929); Wood Stork (*Mycteria americana*) 40 (Kahl 1964) and 130 (Ogden et al. in press); and White Ibis, 22.9 (calculated from Bateman 1970) and 44 (Kushlan 1976b). However, the distribution of distances flown from the colony is known only for the Cattle Egret (Bateman 1970, Siegfried 1971), Wood Stork (Kahl 1964), and White Ibis (Bateman 1970).

In this study we attempt to describe the area used and habitats selected by herons nesting in a colony near Beaufort, North Carolina. Unmarked herons were followed by airplane from the colony to their first landing site. Using this approach, we were able to gather information that indirectly supports the hypothesis that colonies may act as "information centres," wherein unsuccessful birds follow successful ones to better feeding sites (Ward and Zahavi 1973, Krebs 1974).

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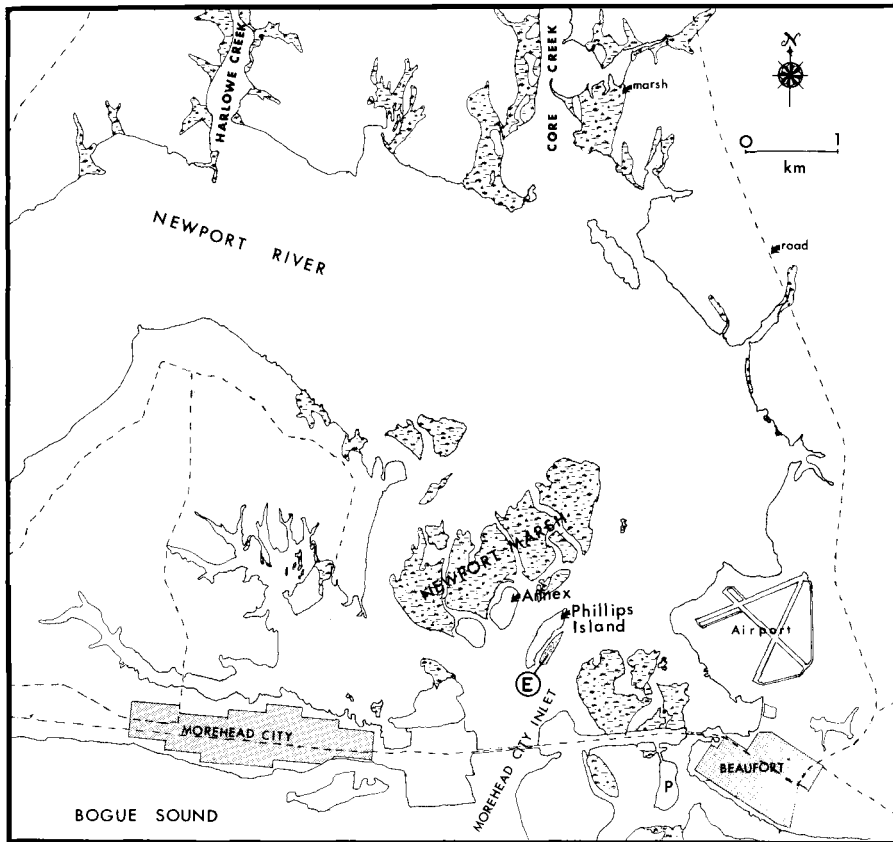


Fig. 1. Newport River Estuary showing Phillips and Annex islands and major areas of *Spartina alterniflora* marsh. P = Pivers Island, E = eelgrass bed southeast of Phillips Island.

STUDY AREA

Our study area was a heronry complex on Phillips and Annex islands near Beaufort, North Carolina (Fig. 1). These two islands are located in the Newport River estuarine system; McCrimmon (1978) gives a detailed description of both sites. Briefly, both islands were formed primarily by dredging—Phillips Island in the early 1900's and Annex Island in the 1950's. The herons nest in maritime shrub thicket encompassing about 1.5 ha on Phillips Island and in a crescent-shaped area of about 4 ha on Annex Island. The colonies are located within the Newport and Causeway marshes, which together make up about 3 km² of *Spartina alterniflora* marsh. The *Spartina* marshes of this area were described by Williams and Murdoch (1969).

Colony population estimates were obtained by doubling a complete count of active nests made in May 1976 (Table 1). The Phillips colony (6 species, 194 adults) had fewer heron species and individuals than the Annex colony (9 species, 2,498 adults); however, there were more Great Egrets (*Casmerodius albus*) in the Phillips colony. Nest initiation was asynchronous among all species within or between colonies (Table 1).

METHODS

During daylight hours (0630–1930) from 7 May to 15 July 1976 we spent 100 h following by airplane (Cessna 172) nine species of unmarked herons, egrets, and ibises from the Phillips and Annex colonies to their first landing site. One or 2 observers in the airplane circled above the colonies at 250–350 m and maintained frequent radio contact with 1 or 2 observers stationed on land or in a boat near the colony.

TABLE 1. Number of adult herons nesting (nest count × 2) in Phillips and Annex colonies in May 1976 and approximate egg-laying date for the majority of individuals of each species in each colony.

Species	Phillips Colony		Annex Colony	
	No. of nesting adults	Date of egg laying	No. of nesting adults	Date of egg laying
Green Heron	—		2	unknown
Little Blue Heron	—		636	late April
Cattle Egret	—		742	early May
Great Egret	126	early April	82	late April
Snowy Egret	16	early April	310	early May
Louisiana Heron	42	early April	420	late April
Black-crowned Night Heron	6	early May	160	early April
Yellow-crowned Night Heron	2	early May	—	
Glossy Ibis	—		44	late April
White Ibis	—		102	late April
Total	192		2,498	

The ground observers were helpful in spotting dark colored birds such as Little Blue Herons, Louisiana Herons, Black-crowned Night Herons (*Nycticorax nycticorax*), and Glossy Ibises (*Plegadis falcinellus*) as they left the colony, and also in distinguishing Cattle Egrets from Snowy Egrets.

We circled the colonies and followed the first individual of a preselected species so that the species samples were stratified over tidal stages, time of day, and season. However, we were unable to sample all species equally because of low numbers for some species and difficulty in following others.

TABLE 2. Description of the first landing site of nine heron species. Species abbreviations are as follows: GREG = Great Egret, WHIB = White Ibis, LOHE = Louisiana Heron, SNEG = Snowy Egret, CAEG = Cattle Egret, LBHE = Little Blue Heron, BCNH = Black-crowned Night Heron, GLIB = Glossy Ibis, YCNH = Yellow-crowned Night Heron.

Habitat ^a	Species									
	GREG	WHIB	LOHE	SNEG	CAEG	LBHE	BCNH	GLIB	YCNH	
Bank <i>Spartina</i>	11		3							
Levee <i>Spartina</i>	9	2				1	1			
Low elevation <i>Spartina</i>	16	14	8	1						
High elevation <i>Spartina</i>	9	58	7	1		1				
Mud flat within <i>Spartina</i>	8	13	14	5		6				
Tidal pond	2		2	1		1				
Mud flat exterior to <i>Spartina</i>	18	5	12	9			1			
Oyster bar	2		1	2						
Tidal creek	19	11	14	3		1	1		1	
High water debris	12	6	7			1			1	
<i>Spartina cynosuroides</i>				1						
Eelgrass (<i>Zostera marina</i>)	13									
Tidal ditch	2	1	2	4		1	1			
Pond hole	1	1	5	2		2		2		
Sand flat	5	6	4	2		1				
Ocean front				1						
Impoundment			1					1		
Pilings and boat riggings	1		2							
Nontidal ditch	3						4			
Fresh water mud pool		6				1				
Fresh water pond	10	6		6			2	2		
Tree	4	10					1			
Field with cattle					12					
Field with tractor					7					
Field					4					
Plowed field					6					
Dump					4					
Habitat not recorded			1							
Total	(472)	145	139	83	38	33	16	11	5	2
Lost in air	(27)	1	2	6	0	2	13	1	2	0

^a Habitat classification modified from Teal 1958, Odum 1961, and Blus et al. 1977

TABLE 3. Tidal level (m) at time of departure from colony for flights by three heron species landing in certain habitats. Listed are $\bar{x} \pm SE$ (n) and results of Student-Neuman Keuls multiple range test. A significant difference ($\alpha = 0.05$) is indicated by means that share no common letters.

Habitat	Species		
	Great Egret	Louisiana Heron	White Ibis ^a
Eelgrass	0.31 \pm .05(13) A		
Tidal creek	0.44 \pm .05(19) AB	0.36 \pm .06(14) A	0.33 \pm .05(11)
Mud flat exterior	0.49 \pm .06(18) AB	0.34 \pm .05(12) A	0.36 \pm .15(5)
Mud flat interior	0.40 \pm .06(8) AB	0.45 \pm .05(14) A	0.30 \pm .05(13)
Sand flat	0.43 \pm .10(5) AB	0.65 \pm .20(4) AB	0.68 \pm .16(6)
Pond hole		0.65 \pm .17(5) AB	
Low elev. <i>Spartina</i>	0.83 \pm .08(16) BC	0.82 \pm .08(8) B	0.55 \pm .09(14)
Trees			0.65 \pm .10(10)
Fresh water	0.83 \pm .08(10) BC		0.61 \pm .11(6)
Bank <i>Spartina</i>	0.78 \pm .09(11) BC		
Mud pool			0.77 \pm .22(6)
High elev. <i>Spartina</i>	1.10 \pm .03(9) C	0.98 \pm .06(7) B	0.72 \pm .05(58)
Levee <i>Spartina</i>	0.99 \pm .11(9) C		
Debris	0.93 \pm .10(12) C	0.88 \pm .11(7) B	0.68 \pm .10(6)

^a No significant difference detected by 1-way ANOVA ($\alpha = 0.05$)

Data on each followed heron included: colony departure time, duration of flight (measured with a stopwatch), description of landing site (see Table 2), association with other birds in flight and at landing site, intra- and inter-specific agonistic behavior at landing site, and use of thermals. If a bird flew off within a few seconds after landing, we followed it to its second landing site while recording full data. Occasionally more than one individual could be followed from the colony simultaneously and the landing sites of all were recorded.

Some of the categories of landing sites (Table 2) require further explanation: (1) *nontidal ditch*—a freshwater runoff ditch near a road or agricultural field; (2) *pond hole*—a depression filled with salt water only at extreme high tides; (3) *freshwater mud pool*—a pool found in fields after recent rains; (4) *impoundment*—a diked brackish basin; (5) *mud flat interior*—mud flat within an area of *Spartina alterniflora*; (6) *mud flat exterior*—mud flat not within *Spartina alterniflora*.

Tidal depth was estimated to 1 cm above or below local mean low tide level at Pivers Island at time of departure. This value was determined by fitting a sine curve to time of day and water depth at high and low tides. These data were obtained from the National Oceanic and Atmospheric Administration laboratory on Pivers Island (Fig. 1), which is about 2.5 km from the two-island heronry. There is some inaccuracy in determining tidal depth of a landing site because herons often flew several minutes before landing and there was as much as 1 h difference in tide levels at different landing sites.

In order to obtain homogeneous variance among means of flight distances, we transformed them to their square roots. In the text and tables, however, the means are squared to present them in their original units.

The rate of travel to the feeding site (a minimum estimate of flight speed) was calculated as the distance between the colony and the landing site divided by flight duration. As herons generally flew directly to the landing site, these are probably accurate estimates of actual flight speed. Flights of less than 3 km were excluded from the flight speed analysis because small errors in the time of departure exaggerated the estimate at these short distances.

For some analyses, tide level was divided into high (≥ 0.48 m) and low tides (< 0.48 m). Preliminary analysis indicated that the 0.48 m water level defined a natural separation of feeding habitats.

Nesting season was divided into three periods, which roughly approximate heron growth data from McVaugh (1972). The early period (7 May–14 June) corresponds to the interval from hatching through the time when the young return to the nest for food; the middle period (15–30 June) begins when the young feed away from the nest but are still unable to fly; and the late period (1–15 July) begins when the young are capable of flight and continues through fledging.

From 16 June to 27 July 1976 we observed herons foraging in a bed of eelgrass (*Zostera marina*) 100 m wide and 500 m long immediately east of Phillips Island (Fig. 1). We observed the number of herons present at 5 min intervals between 2.5 h before and after predicted low tide from a boat nearby or from a spoil area 1 km to the south.

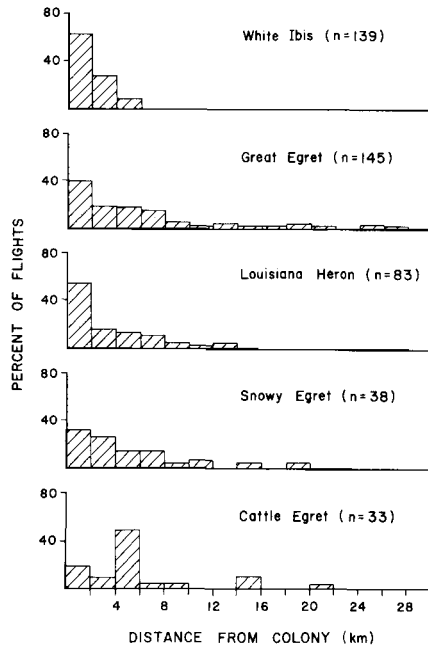


Fig. 2. Percent of flights covering various distances from Phillips and Annex colonies for five heron species.

RESULTS

Habitat use.—We followed 472 individuals of nine species of herons from the Phillips and Annex colonies to their first landing site (Table 2). An additional 27 individuals, including 13 Little Blue Herons and 6 Louisiana Herons, were lost in the air. Feeding habitats differed widely: over 80% of all herons flew to saline habitats, most of which were in the saltmarsh, and only 7% flew to fresh water. Cattle Egrets flew exclusively to fields and dumps (habitats not used by any of the other species). Only Great Egrets flew to eelgrass. Louisiana Herons never flew to fresh water sites.

Habitat use by Great Egrets was dependent on tide level (Table 3). They flew to eelgrass at significantly lower tide levels than to low elevation *Spartina*, bank *Spartina*, high elevation *Spartina*, levee *Spartina*, debris, and fresh water. High elevation *Spartina*, levee *Spartina*, and debris sites were used at significantly higher tides than eelgrass, tidal creeks, mud flats interior, mud flats exterior, and sand flats.

Louisiana Herons selected tidal creeks, mud flats interior, and mud flats exterior at significantly lower tide levels than low elevation *Spartina*, high elevation *Spartina*, and debris sites (Table 3). Tide level had no significant affect on habitat choice for White Ibises.

Distances flown.—Great Egrets, White Ibises, Snowy Egrets, and Louisiana Herons flew most frequently to sites near the colony (0–2 km; Fig. 2). In contrast, Cattle Egrets usually flew 4–6 km. The longest recorded distances (km) by species were: Great Egret, 27.8; Cattle Egret, 20.1; Snowy Egret, 18.3; Louisiana Heron, 13.6; Glossy Ibis, 12.4; Little Blue Heron, 9.5; Black-crowned Night Heron, 7.2; White Ibis, 6.7; Yellow-crowned Night Heron, 1.4.

TABLE 4. Analysis of variance of distance traveled from the colony to the landing site for three heron species.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P
Great Egret					
Main effects					
Daytime	.506	1	.506	<1	<i>ns</i>
Season	.211	2	.105	<1	<i>ns</i>
Tide	4.997	1	4.997	4.076	.043
Interaction					
Daytime × season	.358	2	.179	<1	<i>ns</i>
Daytime × tide	.349	1	.349	<1	<i>ns</i>
Season × tide	3.281	2	1.640	1.640	.265
Residual	164.264	134	1.226		
Total	174.681	143	1.222		
White Ibis					
Main effects					
Tide	.859	1	.859	3.975	.046
Season	.705	2	.353	1.632	.197
Interaction					
Tide × season	.266	2	.133	<1	<i>ns</i>
Residual	28.513	132	.216		
Total	30.693	137	.224		
Louisiana Heron					
Main effects					
Tide	.184	1	.184	<1	<i>ns</i>
Season	3.154	2	1.577	2.163	.120
Interaction					
Tide × season	.729	2	.364	<1	<i>ns</i>
Residual	54.688	75	.729		
Total	58.993	80	.737		

Great Egrets, Black-crowned Night Herons, and White Ibises flew significantly farther at high than low tide—a shift not found in Louisiana Herons, Snowy Egrets, Little Blue Herons, and Cattle Egrets. Great Egret distances, though dependent on tide level, were independent of time of season and time of day (Table 4). Great Egrets flew 2.8 km ($n = 71$) at low tide and 4.3 km ($n = 72$) at high tide. White Ibis distances were dependent on tide level but independent of season (Table 4). White Ibises flew significantly farther at high tide (1.9 km, $n = 61$) than at low tide (1.4 km, $n = 77$). Black-crowned Night Herons also flew significantly farther at high than low tides (high tide = 4.5 km, $n = 6$; low tide = 1.9 km, $n = 5$; t -test, $P = 0.022$). In contrast, distances for Louisiana Herons were independent of both season and tide level (Table 4), and distances flown by Snowy Egrets, Little Blue Herons, and Cattle Egrets were independent of tide level (t -tests, $\alpha > 0.05$).

There were significant differences among species in mean distance flown from the colony (Table 5). Cattle Egrets traveled the farthest ($\bar{x} = 5.68$ km) and White Ibises (at low tide) the least ($\bar{x} = 1.42$ km). Mean distance by species for which we had only small samples were: Little Blue Heron, 2.9 km ($n = 16$); Black-crowned Night Heron (low tide) 1.9 km ($n = 5$), (high tide) 4.5 km ($n = 6$); Yellow-crowned Night Heron, 1.3 km ($n = 2$); Glossy Ibis, 7.3 km ($n = 5$).

Flight speed.—No significant differences were detected among species in rate of

TABLE 5. Mean distance flown (km) from the colony to the landing site by five heron species. A significant overall difference ($\alpha = 0.05$) is indicated by means not sharing a common letter (Mann-Whitney U Test $\alpha = 0.001$).

Species (tide)	Distance (km)	Number of observations
White Ibis (low tide)	1.42 A	77
White Ibis (high tide)	1.90 A	61
Louisiana Heron	2.61 AB	81
Great Egret (low tide)	2.83 AB	72
Great Egret (high tide)	4.28 BC	72
Snowy Egret	3.73 BC	37
Cattle Egret	5.68 C	33

flight to landing sites (Table 6). The mean flight speed for all species was 38.3 km/h and varied from 35.8 km/h for Great Egrets to 45.1 km/h for Glossy Ibises.

Thermals.—Heron species differed in their use of thermals. Little Blue Herons flew in thermals approximately one-third (10 of 29) of the times observed. In contrast, Great Egrets flew in thermals in only 16 of 146 times (11%), White Ibises 3 of 141 times (2%), Glossy Ibises 1 in 7 times (14%), and Louisiana Herons 1 in 89 times (1%). Thermals were never used by Cattle Egrets ($n = 35$), Snowy Egrets ($n = 38$), Black-crowned Night Herons ($n = 12$), or Yellow-crowned Night Herons ($n = 2$). Besides flying farther at low tide, Great Egrets flew farther from the colony when they used thermals (Table 7) but flight speed was the same whether or not they used thermals (t -test, $P = 0.794$). Significant differences in distance flown by Great Egrets in increasing order were: low tide + no thermals (1.92 km, $n = 38$), high tide + no thermals (3.57 km, $n = 64$), low tide + thermals (9.17 km, $n = 11$), and high tide + thermals (18.42 km, $n = 5$).

Behavioral interactions.—Aggressive encounters immediately upon landing were observed for four species. Three of 145 (2%) Great Egrets, 1 of 83 (1%) Louisiana Herons, and 1 of 11 (9%) Black-crowned Night Herons chased away other individuals from their landing area. An additional 5 (3%) Great Egrets, 4 (5%) Louisiana Herons, and 1 of 38 (3%) Snowy Egrets were chased off when they landed.

Cattle Egrets and White Ibises frequently flew to landing sites in groups of two or more individuals. Cattle Egrets flew with conspecifics on 10 of 33 flights (30%) and the White Ibises on 24 of 139 flights (17%). Other species flew in groups less frequently (Snowy Egrets 5%, $n = 38$; Louisiana Herons 5%, $n = 83$; Great Egrets 3%, $n = 145$; and Little Blue Herons 0%, $n = 16$). One Cattle Egret flew slowly out of the colony, appeared to "wait" for another to go by, and followed it to the site. In only one instance did a group include other species: one Louisiana Heron joined another Louisiana Heron and one Little Blue Heron.

TABLE 6. Mean flight speed (km/h) \pm SE for eight heron species. Only flights greater than 3 km were used to estimate rates. ANOVA indicated no significant differences ($P = 0.086$).

Species	Number of observations	Flight speed
Great Egret	67	35.8 \pm 1.09
Cattle Egret	26	37.1 \pm 1.87
Snowy Egret	19	38.6 \pm 2.19
Little Blue Heron	7	38.9 \pm 3.22
Louisiana Heron	32	40.1 \pm 1.90
Black-crowned Night Heron	4	42.0 \pm 4.06
White Ibis	14	44.2 \pm 2.87
Glossy Ibis	5	45.1 \pm 6.04
Overall	174	38.3 \pm 0.75

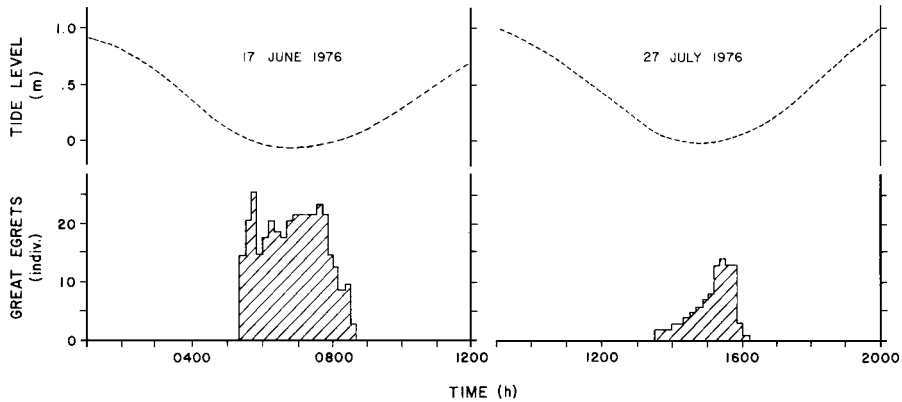


Fig. 3. Number of Great Egrets in the Phillips Island eelgrass bed in relation to tide level on two dates.

Eelgrass beds.—Numbers of Great Egrets feeding in eelgrass peaked during early morning low tides. During 12 low tide observations, the maximum number of Great Egrets in eelgrass beds varied from 10 to 80. Egret usage was significantly greater (t -test, $P < 0.05$) when low tide occurred between 0500 and 0900 ($\bar{x} = 40.5$, $n = 4$) than when it occurred after 0900 ($\bar{x} = 14.9$, $n = 8$). Great Egrets foraged in eelgrass about 1.5 h before or after low tide (Fig. 3). Other species rarely used eelgrass beds. During the 12 watches, Snowy Egrets were present 5 times (maximum present 1,1,2,2,4); Great Blue Herons (*Ardea herodias*) 3 times (1,1,1); Louisiana Herons twice (1,2); and Little Blue Herons once (1).

DISCUSSION

We assume that the first landing site of a heron is indicative of its feeding habitat and distance traveled from the colony. A telemetry study of herons indicated that 51 of 56 feeding locations of White Ibises, 4 of 4 of Little Blue Herons, and 44 of 70 Cattle Egrets were first landing sites (calculated from Bateman 1970). In addition, other studies have suggested that herons return to the same site day after day (Nicholson 1929, Owen 1955, Bateman 1970, and Custer and Osborn unpublished data). We also assume that the airplane did not cause unusual disturbance to the herons. There is an airport within 2.5 km of both colonies (Fig. 1) and air traffic was common. Also, this method has been used successfully by others to follow herons (Hopkins and Dopson 1967, Hopkins and Murton 1969, Browder 1976).

TABLE 7. Two-way ANOVA of distance traveled from the colony for the Great Egret.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F	P
Main effects					
Tide	11.494	1	11.494	13.734	.001
Thermal	49.953	1	49.953	59.687	.001
Interaction					
Tide \times thermal	1.774	1	1.774	2.120	.144
Residual	112.47	134	.837		
Total	169.892	137	1.240		

One limitation of our sampling program is that it did not include nighttime feeding, which is characteristic of Black-crowned and Yellow-crowned night herons. Other species including Great Blue Herons (Milstein et al. 1970, Dennis 1971, Krebs 1974), Wood Storks (Kahl 1964), Reef Herons (*Egretta sacra*, Recher and Recher 1972), and Little Blue Herons (pers. obs.) have been observed foraging at night (Kushlan 1978). However, we suspect that most foraging, except for the night herons, was done during daylight hours.

Great Egrets and Louisiana Herons selected habitats in relation to tide level. Similar shifts in habitat have been observed by others (Kushlan 1978). Krebs (1974) reported that during the winter in Vancouver, British Columbia, when low tides are at night, Great Blue Herons shift from intertidal foraging during the day to hunting for mice in fields and for fish in shallow streams and ditches. Reef Herons forage on reefs at low tide and at high tide either loaf or forage on terrestrial insects, young terns, or food regurgitated by terns (Recher and Recher 1972). Black Skimmers (*Rynchops niger*) feed in pools and mud flats at low tide, but shift to tidal streams and pools as the tide rises (Erwin 1977).

Great Egrets were the only species followed to eelgrass beds in the Beaufort Estuary and the main species seen hunting in eelgrass. We believe water depth to be the critical factor that limits eelgrass use by other species. Great Egrets feed in deeper water than shorter-legged Louisiana Herons and Snowy Egrets (Custer and Osborn 1978). Although we did not measure it, the distance between individual Great Egrets appeared much less in eelgrass than elsewhere. As eelgrass is available for only a few hours at low tide, it may be inefficient for egrets to defend large feeding areas in this habitat. An alternative hypothesis is that prey density may be higher in this habitat than elsewhere, thus attracting more birds.

The availability of feeding sites of Great Egrets, White Ibises, and Black-crowned Night Herons apparently declines around the colony as the tide rises. Consequently, these species travel significantly farther at high than at low tide. Louisiana Herons do not fly farther at high than low tide perhaps because of their habitat preferences. If Jenni's (1969) observation that Louisiana Herons feed along banks or floating vegetation where the water drops off rapidly is true for the Beaufort Estuary, then tide level may not change the availability of suitable feeding sites, and distant flights at high tide would be unnecessary.

Distances herons travel to feeding sites in this study were consistently less than those found by Bateman (1970) at an inland Alabama colony. Our maximum distances of 20.1 km for Cattle Egrets and 6.7 km for White Ibises compared with 28.5 and 22.9 km, respectively, in Bateman's study. Our mean distances for Cattle Egrets (5.7 km) and White Ibises (high tide = 1.9 km, low tide = 1.4 km) were also considerably less than those observed in the Alabama study (Cattle Egrets = 10.6 km, White Ibises = 10.3 km; calculated from Bateman 1970).

As found for the Wood Stork (Kahl 1964, Browder 1976), Great Egrets using thermals move farther from the colony than when they use continuous flapping flight. Travel on thermals may save energy of flapping flight and carry the egret farther to a better feeding territory. As speed is the same with or without thermals, there is some loss of time when using thermals: 25 min per flight at high tide vs. 12 min at low tide. However, increased prey capture rate at a farther site could compensate for the extra time and energy spent in flight.

Our study presents new albeit indirect evidence that heron colonies may act as "information centres," wherein the knowledge of good feeding sites may be com-

municated among individuals (Ward and Zahavi 1973, Krebs 1974). The hypothesis predicts that food resources near colonies are patchy in time and space, and that unsuccessful birds will sometimes follow successful ones to feeding sites. Krebs (1974) collected data that suggested that feeding sites of Great Blue Herons changed daily and that they followed one another to feeding locations. In this study we actually observed several species following conspecifics to feeding sites. Our study also suggests a correlation between the ephemeral nature of food resources and herons following one another. Cattle Egrets flew in groups on almost one-third of their flights and fed in habitats that were changing daily—fields with cattle or tractors and recently plowed fields. In contrast, Great Egrets, Snowy Egrets, Louisiana Herons, Little Blue Herons, and Black-crowned Night Herons generally flew alone and appeared to have feeding sites that were used repeatedly. We observed these species to chase off conspecifics that landed near them and even evict nearby conspecifics upon landing. Also, in a telemetry study Little Blue Herons were repeatedly found in the same location in the Newport Estuary (Custer and Osborn unpublished data). White Ibises followed one another on 17% of their flights, but we lack information on the ephemeral nature of their food resources.

We agree with Ward and Zahavi (1973) that the “information centre” hypothesis is not disproven by solitary feeders nesting in colonies. If the capture rate of a solitary-feeding species declines in a site that it repeatedly uses, it could follow another individual to a new area. Thus, we would predict that shifts in feeding sites would be infrequent in solitary feeders and that they should follow one another less frequently than species that regularly feed in groups. This in fact occurred: the more solitary feeders generally flew alone, but the species that regularly fed in groups (Cattle Egrets and White Ibises) also regularly flew in groups. In addition, the species that we classify as solitary feeders on occasion fed in groups in the Beaufort Estuary. In southern Florida these species commonly feed in groups in fresh water marshes where falling water level concentrates fish (Kushlan 1976b, c).

Ward and Zahavi (1973) describe two systems for information transfer at the colony. The first is “successful first out” and the second “unsuccessful first out.” We recorded one possible case of “unsuccessful first out” for the Cattle Egret: one bird flew slowly out of the colony, appeared to “wait” for another to go by and followed it to the feeding site. Siegfried (1971) also noted this behavior in an African roosting colony of Cattle Egrets.

In summary, our data indirectly support the “information centre” hypothesis. We show a correlation for herons feeding in groups, following one another to feeding sites, and using ephemeral food resources. However, no study, including our own, has yet been able to produce direct evidence that demonstrates unsuccessful birds following successful ones to feeding sites. Until that time, we feel that the hypothesis that colonies can act as “information centres” remains probable but untested.

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LITERATURE CITED

- BATEMAN, D. L. 1970. Movement-behavior in three species of colonial nesting wading birds: A radio-telemetric study. Unpublished Ph.D. dissertation, Auburn Univ.
- BEETHAM, B. 1910. The home-life of the spoonbill, the stork and some herons. London, Witherby & Co.
- BLUS, L. J., S. N. WIEMEYER, J. A. KERWIN, R. C. STENDELL, H. M. OHLENDORF, & L. F. STICKEL. 1977. Impact of estuarine pollution on birds. Pp. 57-71 in Proc. Estuary Pollution Control Assessment Conference (R. Johnson, Ed.). Vol. 1. Washington, D. C., Government Printing Office.
- BROWDER, J. A. 1976. Water, wetlands, and Wood Storks in southwest Florida. Unpublished Ph.D. dissertation, Gainesville, Univ. Florida.
- CRAUFURD, R. Q. 1966. Notes on the ecology of the Cattle Egret, *Ardeola ibis*, at Rokupr, Sierra Leone, W. Africa. *Ibis* 108: 411-418.
- CUSTER, T. W., & R. G. OSBORN. 1978. Feeding-site description of three heron species near Beaufort, North Carolina. Pp. 355-360 in *Wading Birds* (A. Sprunt IV, J. C. Ogden, and S. Winckler, Eds.). New York, National Audubon Society, Research Report No. 7.
- DENNIS, C. J. 1971. Observations on the feeding behavior of the Great Blue Heron. *Passenger Pigeon* 33: 166-172.
- ERWIN, R. M. 1977. Foraging and breeding adaptations to different food regimes in three seabirds: the Common Tern, *Sterna hirundo*, Royal Tern, *Sterna maxima*, and Black Skimmer, *Rhynchops niger*. *Ecology* 58: 389-397.
- HOPKINS, M. N., JR., & C. W. DOPSON, JR. 1967. An aerial search for rookeries in south central Georgia. *Oriole* 32: 39-45.
- HOPKINS, M. N., JR., & P. G. MURTON. 1969. Rookery data from south Georgia. *Oriole* 34: 1-11.
- JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. *Ecol. Monogr.* 39: 245-270.
- KAHL, M. P., JR. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. *Ecol. Monogr.* 34: 97-117.
- KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). *Behaviour* 51: 99-134.
- KUSHLAN, J. A. 1976a. Feeding behavior of North American herons. *Auk* 93: 86-94.
- . 1976b. Site selection for nesting colonies by the American White Ibis (*Eudocimus albus*) in Florida. *Ibis* 118: 590-593.
- . 1976c. Wading bird predation in a seasonally fluctuating pond. *Auk* 93: 464-476.
- . 1978. Feeding ecology of wading birds. Pp. 249-297 in *Wading Birds* (A. Sprunt IV, J. C. Ogden, and S. Winckler, Eds.). New York, National Audubon Society, Research Report No. 7.
- , & M. S. KUSHLAN. 1975. Food of White Ibis in southern Florida. *Florida Field Nat.* 3: 31-38.
- MCCRIMMON, D. A., JR. 1978. Nest-site characteristics among five species of herons on the North Carolina coast. *Auk* 95: 267-280.
- MCVAUGH, W., JR. 1972. The development of four North American herons. *Living Bird* 11: 155-173.
- MEYERRIECKS, A. J. 1962. Diversity typifies heron feeding. *Nat. Hist.* 71: 48-59.
- MILSTEIN, P. LES., I. PRESTT, & A. A. BELL. 1970. The breeding cycle of the Grey Heron. *Ardea* 58: 171-257.
- NICHOLSON, E. M. 1929. Report on the "British Birds" census of heronries, 1928. *Brit. Birds* 22: 270-323, 334-372.
- ODUM, E. P. 1961. The role of tidal marshes in estuarine production. *N.Y. State Conserv.*, June-July: 60-63.
- OGDEN, J. C., J. A. KUSHLAN, & J. T. TILMANT. 1978. The food habits and nesting success of Wood Storks in Everglades National Park in 1974. U.S. Natl. Park Serv., Nat. Sci. Rep. In press.
- OWEN, D. F. 1955. The food of the Heron *Ardea cinerea* in the breeding season. *Ibis* 97: 276-295.
- RECHER, H. F., & J. A. RECHER. 1972. The foraging behaviour of the Reef Heron. *Emu* 72: 85-90.
- SIEGFRIED, W. R. 1971. Communal roosting of the Cattle Egret. *Trans. Roy. Soc. S. Afr.* 39: 419-443.
- SKEAD, C. J. 1966. A study of the Cattle Egret, *Ardeola ibis*, Linnaeus. *Ostrich Suppl.* 6: 109-139.
- TEAL, J. M. 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology* 39: 185-193.
- WARD, P., & A. ZAHAVI. 1973. The importance of certain assemblages of birds as "information centres" for food finding. *Ibis* 115: 517-534.
- WILLIAMS, R. B., & M. B. MURDOCH. 1969. The potential importance of *Spartina alterniflora* in conveying zinc, manganese, and iron into estuarine food chains. Pp. 431-439 in Proc. 2nd Nat. Symp. on Radioecology (D. J. Nelson and F. C. Evans, Eds.). Springfield, Virginia, Nat. Tech. Info. Serv.