THE FEEDING ECOLOGY AND BEHAVIOR OF FIVE SPECIES OF HERONS IN SOUTHEASTERN NEW JERSEY

DAVID E. WILLARD

Theoretically, if two species resemble each other too closely in their requirements, one will have more efficient methods of using the necessary resources and ultimately will drive the second to extinction (Gause 1934). In recent years many field studies have concentrated on documenting differences in resource use between similar species. Schoener (1974) has reviewed many of these studies.

Along the east coast of the United States, south of Long Island, are marshes that support up to eleven species of herons: Great Blue Heron (*Ardea herodias*), Green Heron (*Butorides striatus*), Little Blue Heron (*Florida caerulea*), Cattle Egret (*Bubulcus ibis*), Great Egret (*Casmerodius albus*), Snowy Egret (*Egretta thula*), Louisiana Heron (*Hydranassa tricolor*), Black-crowned Night Heron (*Nycticorax nycticorax*), Yellow-crowned Night Heron (*Nyctanassa violacea*), Least Bittern (*Ixobrychus exilis*), and American Bittern (*Botaurus lentiginosus*). The coexistence of these closely related species makes them an interesting group to examine for methods of sharing resources. Meyerriecks (1960, 1962) investigated behavioral differences between many of these species. My study is a quantitative exploration of the ecological and behavioral adaptations by which some of these herons avoid direct competition for food.

Of the 11 species, 5 seemed not to overlap with others to any great extent. Green Herons, Least Bitterns and American Bitterns hunted primarily in wooded and cattail areas where most of the other species did not venture. Cattle Egrets and Yellow-crowned Night Herons specialized on insects and crabs respectively; these prey represented only small parts of the other species' diets. Black-crowned Night Herons may have competed with other herons for food because they hunted in open areas of the marsh and caught fish of sizes similar to those taken by the remaining species. However, they normally hunted after sunset, and I was unable to gather enough information to include them in the study. This left five species that regularly occurred on the open areas of the marsh and that frequently encountered one another as they hunted: Great Blue Heron, Little Blue Heron, Great Egret, Snowy Egret, and Louisiana Heron.

STUDY SITE AND METHODS

Observations were made at the Brigantine National Wildlife Refuge on the coast of southeastern New Jersey. This marsh has both extensive tidal flats and fresh water impoundments on which herons regularly hunt. A 6.5-km road separates the fresh and salt water. Within the open freshwater marsh are long narrow channels, various-sized potholes, and large pools. The saltwater open marsh has similar channels and potholes, except that their water levels fluctuate with the tides. At the edges of bays are wide expanses of open water with variable wave action depending on the weather.

I watched herons through a 20× spotting scope from inside a car on the dike road. Covering the same route on each trip, I censused the herons by scanning the whole area, and recorded the habitat of all hunting birds. I estimated hunting depth by how far the water was above or below the foot, ankle or leg feathers, and later converted this to actual depth by comparison with leg measurements of heron specimens. If birds were in good view within approximately 150 m, I watched them to determine their feeding methods and their prey sizes, which were estimated by comparing prey length to known bill lengths (Recher and Recher 1972). I watched

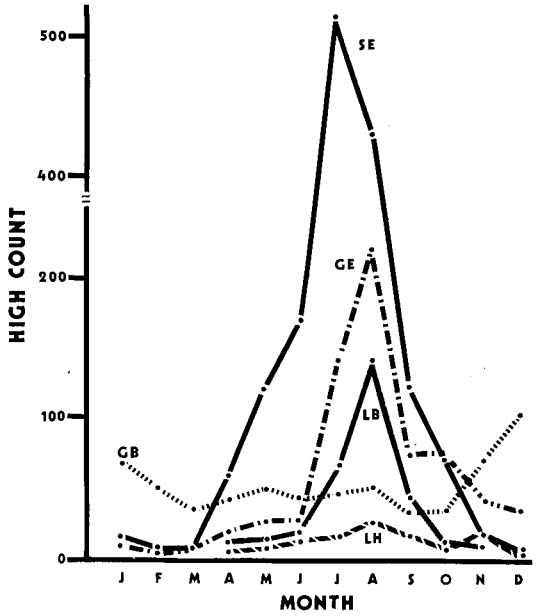

FIGURE 1. Brigantine heron abundances. GB = Great Blue Heron, GE = Great Egret, SE = Snowy Egret, LB = Little Blue Heron, LH = Louisiana Heron. These abbreviations will be used subsequently.

The Condor 79:462–470, 1977

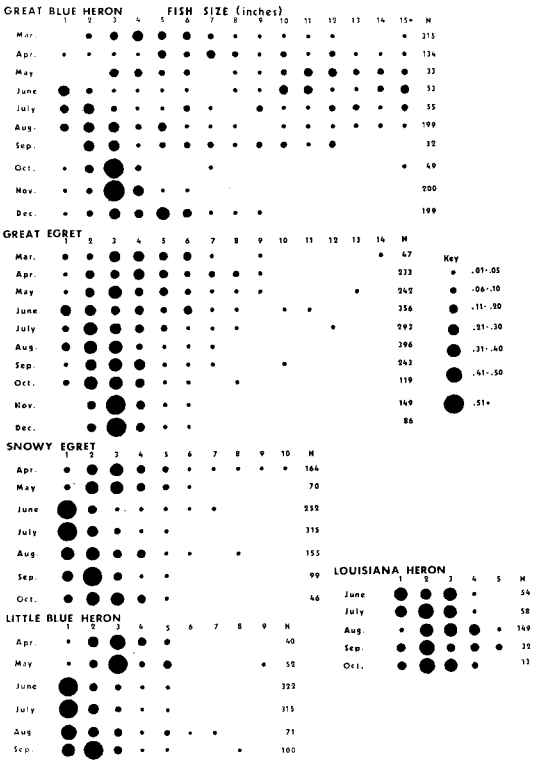

FIGURE 2. Monthly prey-size frequencies.

individuals in the order that they were discovered, and until they flew away, moved out of sight, or stopped feeding. This resulted in more observation time for commoner species and for species with more stationary feeding styles. When I found feeding flocks, I noted flock composition and dynamics.

I visited the marsh on 206 days for a total of 1,380 hours over four years, 1971–1974. I made observations in all months, although more often in March through November. In order to follow seasonal changes, I analyzed the data month by month. Monthly patterns were generally similar from year to year, so I lumped data from months of different years to increase monthly sample sizes. This may have masked some small annual variation in fish dispersion, abundance, and species composition.

In order to compare results for each of the niche variables studied, I chose as a measure of overlap Horn's (1966) modification of Morisita's measure $(2\Sigma p_i q_i)/(\Sigma p_i^2 + \Sigma q_i^2)$ where p_i is the frequency of a given prey size, habitat used, depth hunted, or feeding style for one species, and q_i the frequency for the same variable for a second species. If two species are identical in resource usage, their overlap is 1, and if they are completely different, their overlap is 0. The intermediate numbers give some sense of relative similarity.

RESULTS

HERON ABUNDANCES

Figure 1 shows the monthly abundances of herons at Brigantine. The four-year high count indicates the maximum heron usage of the marsh. Except for the Great Blue Heron, all species peaked during July and August when most of the young left the nests and southern birds came into the area. Great Blue Herons were the most common wintering species. Small numbers of Great and Snowy egrets remained during winter. Louisiana Herons and Little Blue Herons did not normally winter at Brigantine.

FISH SIZE AND SPECIES

The Great Blue Heron had the least overlap with other species for fish sizes taken, particularly during the spring and early summer when it bred and when many of its young first fed on their own (Fig. 2, Table 1). The Great Egret took fish of similar sizes to those taken by the Louisiana Heron, and somewhat larger than the other two small herons. Louisiana Herons differed a little from Snowy Egrets and Little Blue Herons. The latter two took fish of identical size. Recher and Recher (1972) reported percentages of fish sizes in the diets of the small herons in New Jersey. Although their size classes are not directly comparable to mine, our results, on a yearly basis, appear to be similar.

I was able to determine prey species regularly only for fish over 25 cm, which were eaten only by Great Blue Herons and Great Egrets. The primary fish in this size class

TABLE 1. Monthly fish size overlap. Overlaps over .75 with *.

	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
GB-GE	.94*	.64	.53	.68	.73	.94*	.88*	.89*	.99*	.55
GB-SE		.34	.33	.65	.37	.80*	.66	.88*		
GB-LB		.22	.37	.70	.50	.76*	.57			
GB-LH				.59	.65	.87*	.73	.78*		
GE-SE		.81*	.90*	.66	.38	.94*	.73	.78*		
GE-LB		.67	.88*	.70	.55	.79*	.62			
GE-LH				.80*	.89*	.92*	.86*	.97*		
SE-LB		.95*	.84*	.99*	.95*	.95*	.98*			
SE-LH				.74	.57	.72	.97*	.95*		
LB-LH				.82*	.73	.57	.94*			

TABLE 2. Monthly habitat overlap. Overlaps over .75 with *.

	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
GB-GE	.59	.59	.59	.89*	.87*	.97*	.90*	.80*	.80*	.64
GB-SE		.62	.56	.85*	.90*	.96*	.93*	.79*	.43	.82*
GB-LB		.46	.57	.83*	.75*	.75*	.48			
GB-LH		.16	.27	.54	.90*	.90*	.86*	.44		
GE-SE		.99*	.92*	.96*	.95*	.98*	.98*	.98*	.66	.83*
GE-LB		.88*	.58	.78*	.53	.73	.32			
GE-LH		.71	.73	.73	.88*	.92*	.99*	.69		
SE-LB		.91*	.78*	.85*	.74	.78*	.43			
SE-LH		.67	.86*	.69	.88*	.86*	.96*	.79*		
LB-LH		.35	.84*	.58	.68	.55	.31			

were American Eels (*Anguilla rostrata*), White Perch (*Morone americana*), Northern Pipefish (*Syngnathus fuscus*), flounders and sculpins.

HABITAT USE

Great Blue Herons overlapped little with other species in spring months when the others mostly hunted in salt water habitats. In summer and fall, overlaps increased as other species gradually shifted to fresh water habitats. (Table 2, Fig. 3). Great Egrets showed virtually no habitat segregation from Snowy Egrets, very little from Louisiana Herons, and somewhat more from Little Blue Herons.

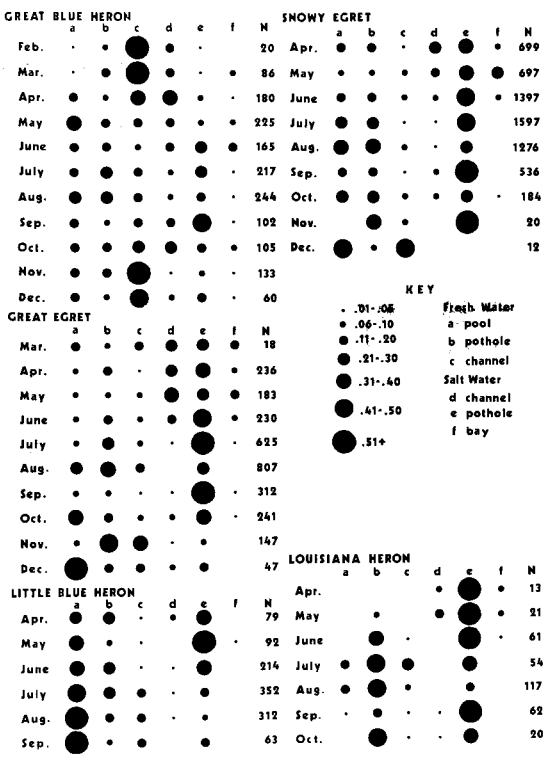

FIGURE 3. Monthly habitat frequencies.

Snowy Egrets used slightly different habitats than either of the other small herons. There was relatively little habitat overlap between Little Blue and Louisiana herons.

HUNTING DEPTH

Great Blue Herons and Great Egrets hunted in similar depths, and both hunted in deeper water than the small species (Table 3, Fig. 4). The three small species all hunted in very similar depths and overlapped greatly. Louisiana Herons did not hunt in deeper water than Snowy Egrets and Little Blue Herons, as Jenni (1969) suggested for Florida birds.

FEEDING BEHAVIOR

Some of the most conspicuous differences between the herons were in their feeding be-

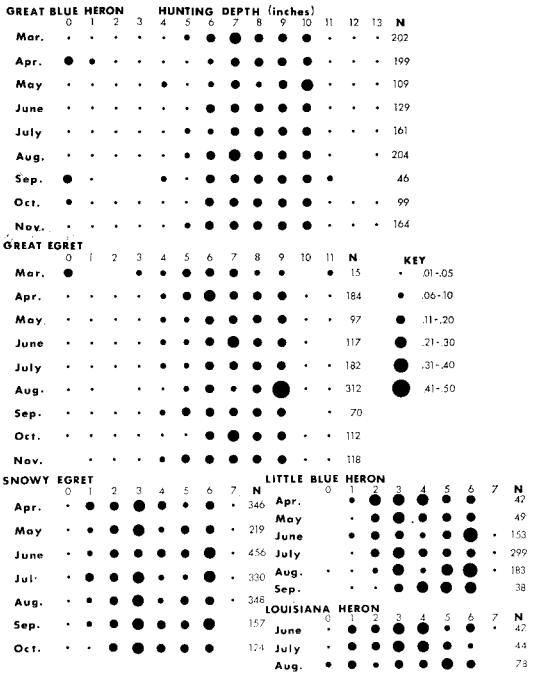

FIGURE 4. Monthly hunting depth frequencies.

TABLE 3. Monthly hunting depth overlap. Overlaps over .75 with *.

	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.
GB-GE	.78*	.81*	.69	.88*	.92*	.65	.80*	.94*	.89*
GB-SE		.42	.28	.42	.28	.35	.32	.26	
GB-LB		.29	.26	.41	.25	.40	.32		
GB-LH				.33	.22	.33			
GE-SE		.61	.41	.53	.44	.25	.52	.31	
GE-LB		.52	.40	.53	.41	.30	.55		
GE-LH				.38	.38	.23			
SE-LB		.92*	.95*	.98*	.85*	.91*	.93*		
SE-LH				.89*	.83*	.90*			
LB-LH				.83*	.96*	.84*			

havior. The literature has many descriptions of these varied techniques (Meyerriecks 1960, 1962, Kushlan 1976). Table 4 is my classification of feeding methods observed at Brigantine, modified from Meyerriecks and Kushlan with several methods that I consider distinct. Figure 5 and Table 5 present summaries of behavioral observations and overlaps between the species.

Great Blue Heron. These herons used upright stand-and-wait and slow-wading equally often. They waded more slowly than any other species and often stopped for long periods before striking or moving on. They usually did not retrace their steps, although occasionally they flew back and covered the same territory again. Active pursuit was infrequent and rarely successful. The one incident of stealing involved chasing a Herring Gull (*Larus argentatus*) away from a fish that the gull was having difficulty swallowing.

Great Egret. This heron's primary hunting method was slow wading. Its pace was faster than that of the Great Blue Heron. Egrets sometimes struck while moving and often swallowed prey as they continued walking. Hunting postures were very similar to those of the Great Blue Heron.

Upright stand-and-wait, another frequent hunting method of Great Egrets, was used mostly amid flooded grass at high tide and when birds were part of large flocks.

Great Egrets rarely used other feeding methods. When actively pursuing, they appeared clumsy with their flapping wings and lunging strikes. Several individuals used head-swaying and one used bill-vibrating. One foot-stirred; this has not been previously reported for this species. Stealing once occurred intraspecifically and once when a Great Egret took a fish from a Snowy Egret. Great Egrets hunt from the air in Louisiana (Rodgers 1974) but I rarely saw them do so; one such bird caught the largest fish (35 cm) that I ever saw this species catch.

Snowy Egret. This species showed the most

TABLE 4. Classification of Brigantine heron feeding behavior.

Standing and Waiting
1. Upright stand-and-wait (after Meyerriecks 1960).
2. Crouched wait: a bird crouches in one spot and strikes horizontally at prey near the water's surface.
3. Bill-vibrating (after Kushlan 1973).

Wade Slowly
1. Regular wade slowly (after Meyerriecks 1960).
2. Foot-stirring or paddling (after Meyerriecks 1960).
3. Head-swaying: a bird sways its head back and forth in an arc with its bill pointed toward one spot, particularly just before striking.
4. Mudflat feeding: regular slow wading, but on mud rather than in water.
5. Sandpiper-style pecking: repeated rapid striking with no apparent orientation toward individual prey items.

Active Pursuit
All feeding methods involving chases; includes open wing and underwing techniques described by Meyerriecks.

Aerial Hunting
Includes diving and hovering (Meyerriecks 1960).

Stealing

TABLE 5. Monthly behavioral overlaps. Overlaps over .75 with *.

	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.
GB-GE	.80*	.56	.93*	.76*	.88*	.93*	.88*	.97*	.47
GB-SE		.49	.56	.60	.50	.83*	.48	.25	
GB-LB		.49	.73	.58	.55	.29	.29		
GB-LH		.84*	.61	.45	.03	.03	.62		
GE-SE		.59	.66	.70	.59	.71	.46	.25	
GE-LB		.95*	.88*	.87*	.68	.18	.33		
GE-LH		.97*	.73	.55	.05	.02	.67		
SE-LB		.58	.65	.70	.48	.30	.16		
SE-LH		.25	.58	.58	.67	.30	.44		
LB-LH		.90*	.70	.53	.06	.02	.23		

varied feeding behavior of any of these herons. Regular slow wading was their most frequent style; the pace was usually faster than that of the previous birds. A Snowy Egret tended to cover an area only once, usually in a fairly straight line.

Foot-stirring was also a frequent hunting technique; it was rare in the other four species. The birds sometimes stood in one spot, shuffling one foot or alternate feet; usually they stirred while walking, shaking their feet with each step and striking as prey was disturbed. Allen (in Palmer 1962) suggested that the egret's yellow feet may actually lure prey rather than frighten it during foot-stirring. The frequent chases that occurred with foot-stirring support Meyerriecks' (1959) view that this feeding method disturbs prey into motion.

Hunting with foot-stirring altered this egret's diet. Most of the prey that I identified during this feeding method were juvenile eels and large prawns, prey items not usually taken by other herons. In addition, foot-stirring yielded many prey that were too small for me to identify, with the egret's swallowing often the only indication that a strike was successful. When I dip-netted in places where egrets had been vigorously foot-stirring, I caught mostly small prawns, amphipods and larval insects. I did not always record the numbers of prawns and young eels taken, but in 1974 alone, I saw Snowy Egrets capture at least 300 2–3 cm prawns and 145 elvers. The large numbers (34% of observed 1974 diet) of these prey make them a significant and distinctive part of the Snowy Egret diet.

Snowy Egrets relied on active pursuit more than any other heron except for the Louisiana Heron. Pursuit involved galloping chases, flapping wings, and many quick turns. Usually an egret ran back and forth, small fish often jumping out of its path. Strikes were frequent, missing more often than not. After a strike, the bird usually paused, appearing to relocate prey, and then continued pursuit. No stealth was involved and everything about this feeding method suggested that its object was to confuse the fish.

The Snowy Egret was the only species that regularly hunted on mudflats that were exposed at low tide. The only prey that I saw taken there were 15–20 cm annelids. An egret walked slowly in the mud and pecked for these long worms. The captured worm was dipped in the water, shaken until it fragmented, and then picked up and swallowed. I scrutinized the mudflats, trying to spot these worms, but never saw any revealing movement nor caught any worms with random swipes with a dip net. The egrets found them in abundance however, and almost never

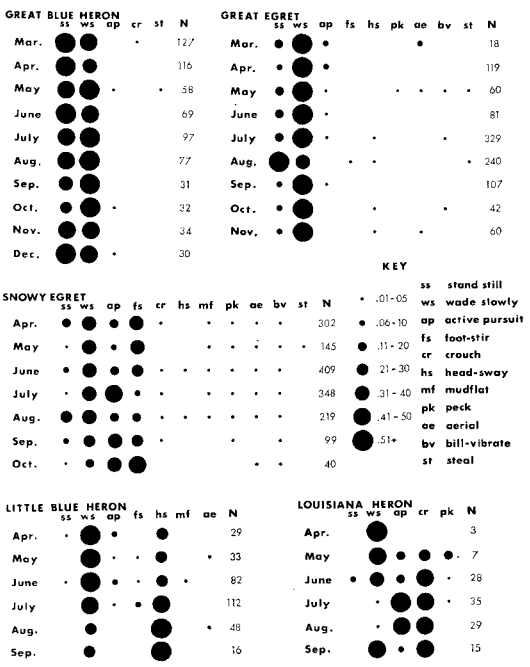

FIGURE 5. Monthly behavioral frequencies.

missed when striking on mud. From April through August 1974, I saw Snowy Egrets take more than 240 annelids (18% of identified prey items), so worms also formed a large part of the diet.

Snowy Egrets stood and waited when they were part of large feeding flocks and when they crouched on land and struck at fish breaking the surface of fresh water channels. Bill-vibrating was infrequent and nearly restricted to this species. Sandpiper-style pecking was also largely confined to these egrets. The birds struck repeatedly while walking, without any preparation, but they rarely seemed to capture anything. The technique resembled feeding behavior of the Greater Yellowlegs (*Tringa melanoleuca*) at Brigantine. Once an egret took a fish from a Glossy Ibis (*Plegadis falcinellus*).

Little Blue Heron. These herons hunted most frequently by wading slowly and peering closely. They kept their bills close to the water at all times and constantly tipped their heads as they peered around vegetation and under banks (peering over, Meyerriecks 1960, 1962). They moved in zigzag patterns and frequently turned and traversed an area again.

Often a heron fixed its bill in one spot, sometimes even touching the water's surface, and then swayed its head in an arc around this point. Head-swaying seemed to occur only after the heron had spotted prey, and since the following strikes tended to be deep, it probably served to adjust for parallax. Of the herons I watched, only this species used this method regularly.

Little Blue Herons rarely used other feeding methods. They occasionally foot-stirred, which is not generally reported for this species. Active pursuit and aerial hunting were infrequent. I saw no extended periods of aerial hunting such as Mock (1974) found in Texas.

Louisiana Heron. The primary feeding method of this species was to crouch at the edges of channels and potholes, and to strike nearly horizontally at the water's surface, skimming off a fish or tadpole. The crouch was often very deep, sometimes with the curve of the neck and breast feathers touching the water. After a lunging strike, a bird usually returned to the edge of the water and crouched again. Often it moved along the edge so that each crouch was in a new spot. The birds often flew to a new spot after several strikes in one area, making them the most difficult heron to watch for long periods.

Active pursuit occurred almost as frequently as crouched waiting, and took two forms. One form resembled the active hunting by Snowy Egrets, with loping chases, flapping wings and lunging strikes. In the second form, which I saw only in the Louisiana Heron, a bird spread one wing and struck as it turned in tight circles in the direction of the open wing (pirouetting, Meyerriecks 1962). Sequences were repeated quickly, and the bird either turned in the same direction with the same wing extended, or else extended the other wing and turned in that direction. Like other forms of active pursuit, this feeding method involved no stealth, and probably confused prey.

Louisiana Herons also fed by regular slow wading, but they were the only herons for which this was not the main technique. Upright stand-and-wait and sandpiper-style pecking were both unusual.

FEEDING AGGREGATIONS

At Brigantine, from April through October, there were frequently aggregations of feeding birds, ranging from 5 to 600 individuals. Eighteen species occurred in a fish-eating assemblage at least once (Table 6). In these flocks, the birds fed in their normal manners: terns dived from the air, skimmers glided at the surface, and ibises probed amid herons that were posing or chasing as when alone. Of the 196 flocks observed, I saw 49 different combinations of herons and ibises. Flocks with four species or less were the most usual.

Many flocks seemed to be composed of one or several common species at the center, and several individuals of other species at the periphery. This pattern has also been reported for flocks of forest insectivores (Krebs 1973). Snowy Egrets and Glossy Ibises were most frequently the central species and also the two most often forming single-species flocks. Occasionally they were at the edges of flocks with Great Blue Herons or Great Egrets in the middle. Little Blue Herons, Louisiana Herons and Black-crowned Night Herons were usually peripheral species, although immature Little Blue Herons sometimes formed single-species flocks.

I watched some of these flocks to see whether some species left earlier than others and whether some remained after most had left. It seemed possible that one species might be the best discoverer of a new food source, that others might move in when the food had been little exploited, and that others might be efficient at gleaning what was left, as Kruuk (1967) observed for vultures. Determining the first members of a flock was dif-

TABLE 6. Percent of heron flocks containing various species.

Great Blue Heron	30	Greater Yellowlegs	2
Green Heron	1	Herring Gull	2
Great Egret	55	Laughing Gull	15
Snowy Egret	85	Forster's Tern	8
Little Blue Heron	37	Common Tern	13
Louisiana Heron	19	Least Tern	3
Black-c. N. Heron	11	Black Tern	1
Glossy Ibis	49	Black Skimmer	6
Red-breasted Merganser	1	River Otter	1

ficult. I saw flocks form only twice: once around a small group of feeding terns and once around a lone Louisiana Heron that had been striking frequently. Many flocks included neither terns nor Louisiana Herons, so more observation is needed to see whether there is a pattern to flock formation. I saw the dissipation of flocks more often, and no species was consistently the last. Usually the flock diminished gradually, roughly in proportion to the numbers that were present when I began observing.

DISCUSSION

FOOD SEGREGATION

June through September tended to be the months of greatest habitat overlap (Table 2). They were also months of occasionally high overlaps in size of fish (Table 1), so that food source segregation was not always obvious. Overlap in behavior decreased during this period (Table 5). If different feeding methods lead to different prey, the fairly low overlaps in late-summer behavior may reflect a large degree of prey-species specialization that is masked by the high overlaps in prey-size. Behavioral overlaps tended to be greatest in spring and early summer. In late summer and fall, Snowy Egrets, Little Blue Herons and Louisiana Herons each relied heavily on special modes of behavior such as active pursuit, crouched waiting or head-swaying.

The behavioral specialties probably do lead to differences in the prey taken. The very long periods of standing motionless that are typical of the Great Blue Heron should facilitate the finding and capture of many of its large prey such as White Perch and American Eels, which are themselves active predators (Bigelow and Schroeder 1953). When a Great Blue Heron took bottom-dwelling sedentary fish such as flounders and sculpins, the strike was always preceded by regular slow wading. Krebs (1974) found this to be the predominant feeding method in an area where these fish were the main prey. The Great Egret's steady slow walking led to an intermediate-sized prey that was more abundant, if its greater striking rate (.9 versus .2 strikes/min) can be taken as a rough indicator of prey availability. A more active hunting technique should be better adapted to finding prey that is evenly distributed and less mobile, as one might expect with some smaller fish (Lotrich 1975). The most interesting differences are among the feeding methods of the three smaller herons since the fish and tadpoles that they took were of similar sizes. The foot-stirring and mudflat-feeding of the Snowy Egret procured a set of invertebrates and elvers that was virtually unexploited by the other herons. The two forms of active pursuit that were common in Snowy Egrets and Louisiana Herons apparently allowed exploitation of open water prey that were more easily captured when confused. These were prey that Little Blue Herons rarely exploited. The stealthy crouched waiting with horizontal strikes of the Louisiana Heron exploited fish that swam just below the surface, while the Little Blue Heron's head-swaying followed by deep forceful strikes focused on prey that was near the bottom. The peering of the Little Blue Heron may be well adapted for hunting in thick vegetation where prey can easily hide. These species may only rarely ignore an available fish, and there is definitely some overlap in the prey species captured (e.g., all species took eels on some occasions), but the various feeding methods are probably differentially efficient at finding and capturing different types of prey. Jenni (1969) found that a variety of prey species was taken by Snowy Egrets, Little Blue Herons and Louisiana Herons. All of them took occasional individuals of most of the prey, but the most common prey species was different for each heron. Jenni worked in Florida where some of the available prey species differ from those on the New Jersey coast (Bigelow and Schroeder 1953), but I suspect that the behavioral differences among the New Jersey herons led to similar differences in prey.

FEEDING AGGREGATIONS

Four possible adaptive values of feeding flocks in birds have been proposed. First, a flock may find clumped food sources that are too large for one individual to exploit completely. Great Blue Herons in flight are sometimes attracted to birds already feeding

in tidal pools where prey is concentrated (Krebs 1974). Great Tits (*Parus major*) and chickadees move to areas where there are successful individuals, and feeding in a group increases an individual's chance of finding food (Krebs et al. 1972, Krebs 1973). Flocks of mixed species may combine the foraging skills of the species and increase the total scanning range of the flock (Krebs 1973). A second adaptive value may be improved predator defense. When more eyes are involved, more time per individual can be spent feeding rather than looking around for predators (e.g., Moynihan 1962, Lack 1968, Willis 1972). In some cases it has been shown that flocking birds look around less than lone birds (Powell 1974). A third possibility is that a flock can gauge where to move next, avoiding search time in recently depleted areas. Once a flock has moved through an area, it will be obvious that the area is not worth searching the next time the flock comes by (Cody 1971). The fourth possibility is that the feeding actions of one bird may disturb prey that another can subsequently catch (Rand 1954).

At Brigantine, it is unlikely that heron aggregations provide defense against predation. Marsh Hawks (*Circus cyaneus*) are the only potential avian predators present during the main flocking season, and a Snowy Egret or Little Blue Heron is near the upper size limit of prey for this species. Bent (1937) reported Marsh Hawks taking an American Bittern and a Green Heron, but prey of this sort is extremely rare compared to small bird and mammalian prey. If predator defense were an important current or historic function of these flocks, one would expect isolated individuals to spend much time looking around. Instead, their attention seems intensely focused on feeding whether the birds are in flocks or alone.

It is also unlikely that these birds are flocking to gauge what part of the food supply has been depleted. This would be more possible for birds feeding on stationary seeds (as suggested by Cody 1971) than for birds feeding on prey as transient as schooling or spawning fish.

At Brigantine, there are two probable advantages for a heron to join a flock: (1) finding abundant and inconstant food supplies, and (2) increasing the number of prey confrontations owing to disturbances by other members of the flock. Fish sometimes school or congregate to spawn, and receding tides often leave fish trapped in potholes. These clumps of food are present for only a matter of hours in the case of tidal pools; the clumps may contain enough food for several to many birds. When herons see others feeding successfully, they may increase their own success by exploring the same area. If there is more food than the first individual can use, it may not be disadvantageous for him to be conspicuous enough for others to find him and to lower his normal aggressiveness so that they are able to join. Also, a lone bird's success rate may increase when it is joined by others. At Brigantine, nearly 90% of the feeding aggregations contain either Snowy Egrets or Glossy Ibises. The former, with their active feeding styles, and the latter, with their constant probing, probably stir up prey that a single hunter does not see as it escapes. When a prey item in a heavy concentration escapes from one Snowy Egret, it may become available to an opportunistic neighbor. Glossy Ibises never chase prey, so that anything stirred up as they probe is free to be taken by other herons. Prey that act so as to avoid one species of heron may expose themselves to predation by a second species with different hunting methods.

SUMMARY

Five species of herons that I watched in southeastern New Jersey appeared to segregate with respect to their food source. Great Blue Herons ate many fish that were too large for any of the other species to take. Great Egrets took moderate-sized fish, some of which were larger than the three smaller herons could handle. They also fed in deeper water, so that the small fish that they captured may not have been available to the smaller herons. Snowy Egrets, Little Blue Herons and Louisiana Herons fed on fish of similar sizes. Louisiana Herons and Little Blue Herons showed some major habitat differences, but the small herons differed even more in behavior. Each fed in special ways that the others rarely used. The Snowy Egret was the species most likely to aggregate in large numbers at apparently temporary food sources such as tidal pools. Snowy Egrets and Louisiana Herons often fed by active pursuit. Little Blue Herons almost never fed this way. Snowy Egrets frequently foot-stirred and hunted on mudflats. Both of these methods yielded large numbers of invertebrate prey that neither Little Blue nor Louisiana herons caught. Louisiana Herons crouched at the edge of banks and struck nearly horizontally at prey near the water's surface; Little Blue Herons

swayed their heads and then struck deeply and vertically at prey near the bottom.

ACKNOWLEDGMENTS

Henry Horn, Douglas Mock, Peter Feinsinger, Mark Konishi, John Terborgh, and Egbert Leigh read early drafts of this work, and gave extremely helpful comments. John Jaenike, Debra Moskovits and John Fitzpatrick shared bird watching trips, and their ideas often helped me to look at heron and ecology matters in new ways. My work was supported by a NIH predoctoral traineeship administered through Princeton University.

LITERATURE CITED

BENT, A. C. 1937. Life histories of North American birds of prey. U.S. Natl. Mus. Bull. 170:1–482.

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Fish. Bull. 53.

CODY, M. L. 1971. Finch flocks in the Mohave Desert. Theor. Popul. Biol. 2:142–158.

GAUSE, G. F. 1934. Struggle for existence. Hafner, New York.

HORN, H. S. 1966. Measurements of "overlap" in comparative ecological studies. Am. Nat. 100: 419–424.

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.

KREBS, J. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). Can. J. Zool. 51:1275–1288.

KREBS, J. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron. Behaviour 51:99–151.

KREBS, J., M. H. MACROBERTS, AND J. M. CULLEN. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. Ibis 114: 507–530.

KRUUK, H. 1967. Competition for food between vultures in East Africa. Ardea 55:171–193.

KUSHLAN, J. A. 1973. Bill-vibrating. A prey attracting behavior of the Snowy Egret, *Leucophoyx thula*. Am. Midl. Nat. 89:509–512.

KUSHLAN, J. A. 1976. Feeding behavior of North American herons. Auk 93:86–94.

LACK, D. 1968. Ecological aspects of reproduction in birds. Methuen, London.

LOTRICH, V. A. 1975. Summer home range and movements of *Fundulus heteroclitus* (Pisces: Cyprinodontidae) in a tidal creek. Ecology 56: 191–198.

MEYERRIECKS, A. J. 1959. Foot stirring behavior in herons. Wilson Bull. 71:153–158.

MEYERRIECKS, A. J. 1960. Comparative breeding behavior of four species of North American herons. Publ. Nuttall Ornithol. Club 2:1–158.

MEYERRIECKS, A. J. 1962. Diversity typifies heron feeding. Nat. Hist. 71:46–57.

MOCK, D. 1974. Aerial hunting by Little Blue Herons. Wilson Bull. 86:280–282.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithson. Misc. Collect. 143: 1–140.

PALMER, R. S. 1962. Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven.

POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by Starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim. Behav. 22:501–505.

RAND, A. L. 1954. Social feeding behavior of birds. Fieldiana Zool. 36:1–71.

RECHER, H. F., AND J. A. RECHER. 1972. The foraging behavior of the Reef Heron. Emu 72:85–92.

RODGERS, J. A. JR. 1974. Aerial feeding by Snowy Egrets and Great Egrets in Louisiana waters. Wilson Bull. 86:70–71.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

WILLIS, E. O. 1972. The behavior of Spotted Antbirds. Ornith. Monogr. 10.

Department of Biology, Princeton University, Princeton, New Jersey 08540. Accepted for publication 15 November 1976.